EPIDERMAL STRUCTURE OF SOME MEDULLOSAN *NEUROPTERIS* FOLIAGE FROM THE MIDDLE AND UPPER CARBONIFEROUS OF CANADA AND GERMANY

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ABSTRACT. Cuticles from seven taxa of neuropterid frond are described. Based on these and earlier descriptions, four main groups of species are recognized within *Neuropteris* Brongniart: Group I – *N. loshii* Brongniart, *N. tenuifolia* Sternberg and *N. rarinervis* Bunbury; Group II – *N. ovata* var. *simonii* (Bertrand), *N. ovata* var. *sarana* (Bertrand), *N. ovata* var. *aconiensis* nov. var., *N. flexuosa* Sternberg and *N. schaeferi* Doubinger and Germer; Group III – *N. scheuchzeri* Hoffmann, *N. macrophylla* Brongniart, *N. subauriculata* Sterzel, *N. britannica* (Gutbier), *N.* sp α Barthel and *N.* sp β Barthel; Group IV – *N. neuropteroides* (Göppert). The groups may correspond to more refined form-genera but, in the absence of epidermal evidence for certain key species including the type *N. heterophylla* Brongniart, no formal proposals are made here. The epidermal evidence suggests that most of the fronds were from plants growing in a moist, lowland environment. Only one (*N. scheuchzeri* Hoffmann) shows evidence of having occupied a more elevated habitat.

FRAGMENTS of medullosan pteridosperm foliage are abundant in the middle and upper Carboniferous of North America, Europe and Asia. They are broken pieces of large fronds (some originally over seven metres long (Laveine 1986)) from plants mostly growing on river levées (Gastaldo 1987; Zodrow and Cleal 1988). The fragments were probably detached from the plant during storms and are usually found in mudstones deposited in interdistributary bays between the river channels (see Fielding 1984, 1986 for details of the sedimentology).

Classifying such fossils presents several difficulties. Although the seeds and pollen organs were originally attached directly to these fronds, they usually became detached during fossilization (for rare exceptions see Stidd 1981). Evidence for the form and structure of the stems which bore the leaves is also limited. It may be difficult to determine even the overall structure of these large fronds, as has been done for some of the smaller-leafed pteridosperms (e.g. *Mariopteris* – Boersma 1972). The character set usually available for classifying the medullosan fragments is thus extremely limited, being restricted mainly to the form and nervation of the pinnules and the structure of the ultimate, and sometimes the penultimate and antepenultimate, pinnae.

An additional source of potentially useful characters is the cuticle. If the thermal history of the preserving sediment has not been too extreme (at least 28 % of the volatile components must be retained in the coalified tissue (Barthel 1962)), the cuticles may still be preserved and show a number of structures, including the stomata. Since available characters are so limited, the additional features supplied by the cuticle can take on a greater significance than they would in the study of extant plants (Meyen 1987). In fact, Hill (1986) has argued that the epidermis has no special taxonomic status in extant plants, and that its significance can only be properly judged in the light of the structure of the whole plant. Nevertheless, cuticle studies are now a well established part of the investigation of Mesozoic pteridosperm foliage (e.g. Townrow 1960; Harris 1964).

Cuticles are described from medullosan foliage of the form-genus *Neuropteris* Brongniart (1822). The first records of cuticles from this form-genus date from early in this century (Wills 1914; Gothan 1915; Bolton 1929), but they are not easy to interpret. Wills figured one of the pinnules which she analysed, but it clearly came from near a pinna terminal, making it difficult to identify.
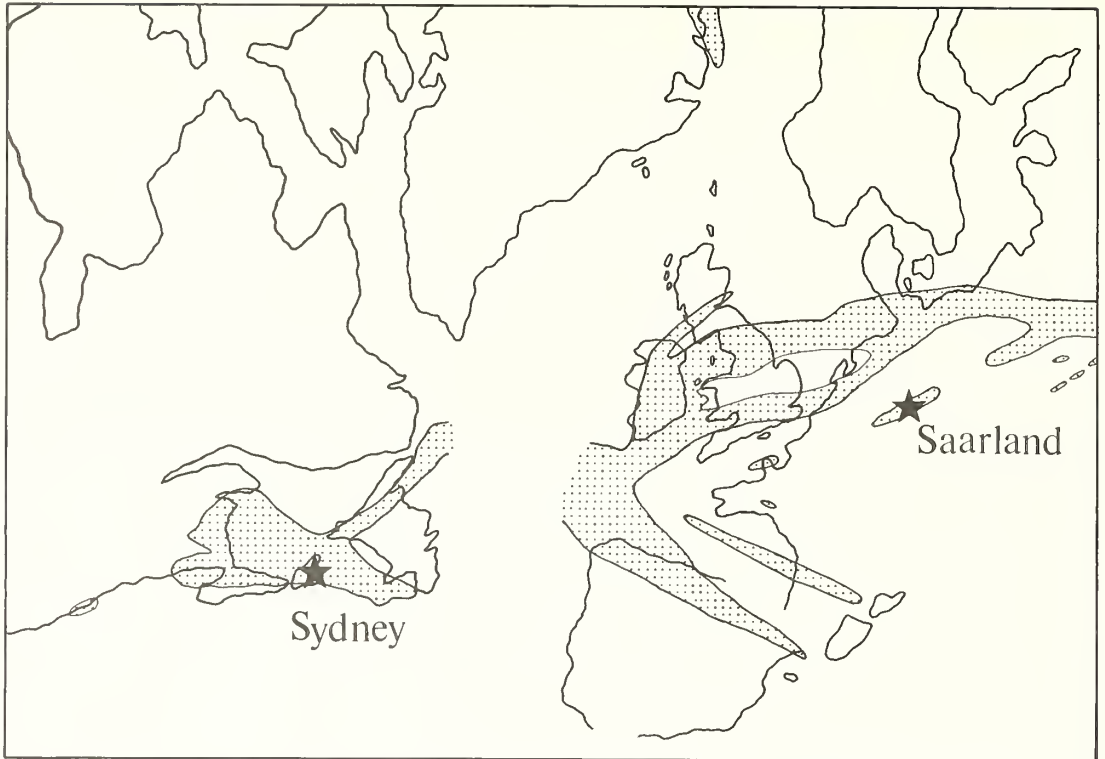
TEXT-FIG. 1. Palinspastic map showing what is now the North Atlantic area during the Westphalian D. Main areas of sedimentation shown by stippling. Two areas from where cuticles described in this paper originated are shown by stars. Based on Zodrow and Cleal (1985, fig. 1). Scale approximately 1:30 000 000.

Gothan figured only the cuticles, whilst Bolton figured neither cuticles nor hand specimens, making it difficult to verify species identifications. Bolton's work is particularly suspect. She concluded that all of the 'species' examined had very similar epidermal structures. This is difficult to reconcile with the results of subsequent studies, including the present one. However, her earlier paper on the gross-morphology of the specimens (Bolton 1926) showed that she was using a variety of species names for different pinnule forms of *Neuropteris tenuifolia* Sternberg (cf. also comments by Crookall 1959, p. 95), explaining the anomalous consistency in epidermal structures. Guthörl (1941) illustrated a cuticle of a neuropterid from the Saarland Coalfield, without figuring the hand specimen to establish its identity.

The most important contributions to the subject are by Barthel (1961b, 1962, 1976) and Reichel and Barthel (1964), who described and illustrated cuticles from eleven species with neuropterid pinnules. Our only significant disagreement is with Barthel's identification of a specimen as *Neuropteris obliqua* (Brongniart), which according to Laveine (1967) probably belongs to *N. loshii* Brongniart. Barthel's results are used as the starting-point for our comparisons of the new material described here. Other recent records of neuropterid cuticles are by Daber (1963) and Dollé and Laveine (1965), and in unpublished theses by Saltzwedel (1968) and Cleal (1985). Finally, epidermal features are known from some permineralized neuropterid pinnules (Reihman and Schabilion 1978; Oestry-Stidd 1979; Beeler 1983; Schabilion and Reihman 1985).

Our specimens are from Westphalian D to early Cantabrian floras, when fossil plants have a considerable biostratigraphical significance (Laveine 1977; Wagner *in* Wagner *et al.* 1983; Cleal 1984a), making it essential that their taxonomy is thoroughly understood. The cuticles may help
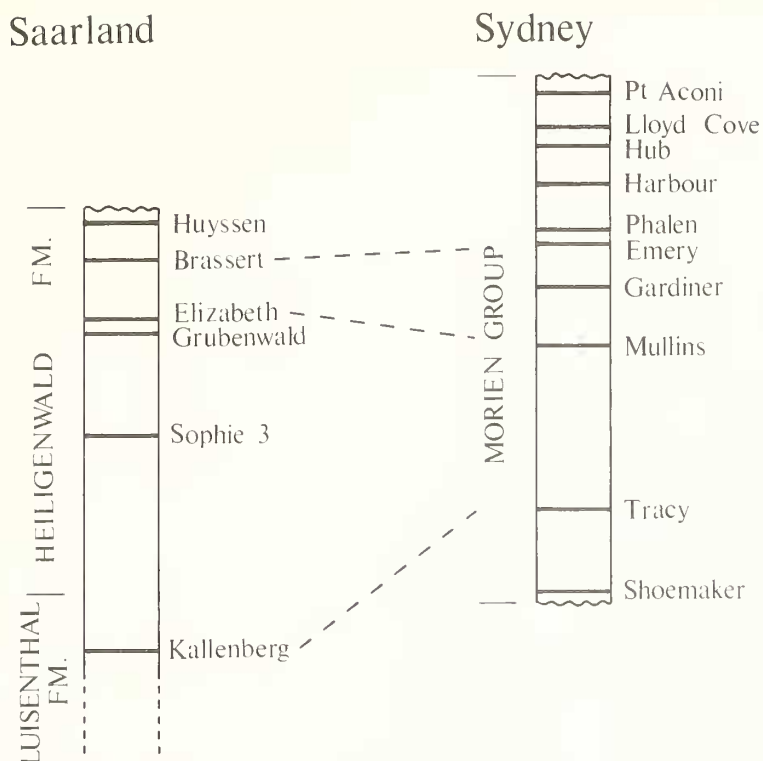
TEXT-FIG. 2. Correlation between Westphalian D sequences of the Saarland and Sydney coalfields, based on data given in Cleal (1984b) and Zodrow and Cleal (1985).

establish the taxonomic position of the form-genus and resolve any non-homogeneities within it resulting from our limited knowledge of the frond architecture. The cuticles may also provide information of palaeoecological significance.

MATERIAL

Full details of the provenance of the specimens are given in the appendix. They originated from the Saarland Coalfield, Federal Republic of Germany, and the Sydney Coalfield, Nova Scotia, Canada (text-figs. 1 and 2). The cuticles from the former were prepared from specimens stored in the Saarbrücken mining school museum, von der Heydt, near Saarbrücken (Cleal 1985), but now housed in the main part of the mining school in Saarbrücken. They are assigned catalogue numbers prefixed by 'C/', which identifies them as Carboniferous plant fossils. The cuticles from these specimens are in the Department of Palaeontology, British Museum (Natural History), London, under catalogue numbers prefixed by 'V'. Relevant stratigraphical details are given by Cleal (1984b).

The specimens and figured cuticles from the Sydney Coalfield are in the collections of the University College of Cape Breton. They are assigned catalogue numbers, whereby three numbers indicating the year of collection are followed by the letters GF, and are in turn followed by the number of the specimen collected that year (e.g. 980GF-200 is the 200th specimen collected in 1980). A representative collection of the non-figured Canadian cuticle preparations has been presented to the British Museum (Natural History). Biostratigraphical details for this coalfield are given by Zodrow and Cleal (1985) and Zodrow (1986).
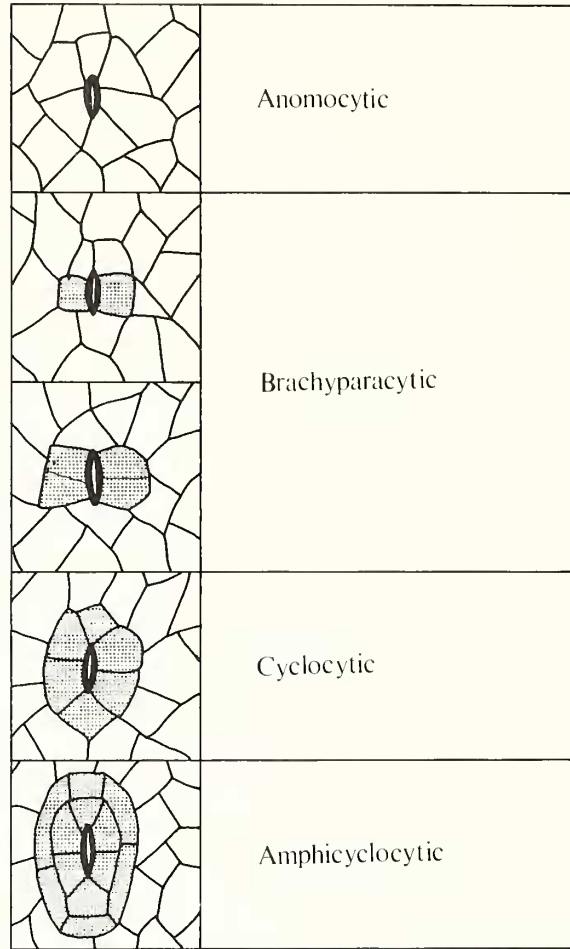
TEXT-FIG. 3. Diagrammatic representations of the principal types of stomatal apparatus mentioned in this paper. Subsidiary cells shaded with stippling, and guard cells marked with thick black lines.

METHODS AND TERMINOLOGY

Cuticles were prepared from the compression fossils as described by Barthel (1961 a, 1962). The compressions were separated from the rock using 50 % hydrofluoric acid, and then macerated in Schulze Solution (potassium chlorate dissolved in nitric acid), usually diluted to 30–50 % with water. They were subsequently washed in 5 % potassium hydroxide and then rinsed in distilled water. Abaxial and adaxial cuticles were separated using fine needles, and then mounted in glycerine jelly, in which safranin dye was dissolved.

The prepared cuticles were examined by optical transmission microscopy. The staining of the cuticles allowed unpolarized light to be used for some observations, but in most cases Nomarski Contrast (polarized phase contrast) improved the resolution. Photographs were taken using a 35 mm camera attachment to the microscope, and drawings made with a *camera lucida* attachment.

The terminology outlined by Dilcher (1974) for angiosperm cuticles has been used here. In particular, the classification of the fully-developed stomatal apparatus was found to be preferable to the various ontogenetic schemes that have been proposed (e.g. Florin 1931; Pant 1965) since such developmental information is rarely shown in fossil leaves (Wilkinson *in* Metcalfe and Chalk 1979; Meyen 1987). Four main types of stomatal apparatus have been found in the neuropterids, and are summarized in text-fig. 3.

The style of taxonomic classification adopted is as outlined by Cleal (1986). In particular, a rather more

loosely defined concept of the form-genus is used than that given in the International Code of Botanical Nomenclature. This has the advantage of allowing the taxonomy to dictate the nomenclature, rather than the other way round as is the case with the form-genus defined in the ICBN. An essentially similar concept of form-genus was independently developed by Visscher *et al.* (1986) in a study on Palaeozoic conifers. Another concept used is that of the Satellite Taxon (Meyen 1978; Thomas and Brack-Hanes 1984). Such a taxon is assigned to a higher ranking taxon only if the evidence allows, and there is no necessity to assign it to a taxon of intermediate rank. In the present study, for instance, *Neuropteris* is regarded as a satellite form-genus of the order Trigonocarpales, but there is as yet insufficient evidence to place it in a particular family.

SYSTEMATIC PALAEONTOLOGY

Division PINOPHYTA Meyen (1987)
Class CYCADOPSIDA Meyen (1987)
Order TRIGONOCARPALES Meyen (1987)
Satellite form-genus NEUROPTERIS (Brongniart) Sternberg emend. Zodrow and Cleal (1988)

Type species. Neuropteris heterophylla Brongniart emend. Laveine (1967).

Remarks. This is one of the most widely reported form-genera from the Carboniferous adpression floras (*sensu* Shute and Cleal 1987). The most comprehensive taxonomic analysis is given by Laveine (1967), who placed particular emphasis on its frond architecture. Cleal (1985) and Zodrow and Cleal (1988) have reviewed the available evidence on frond architecture and an emended diagnosis was proposed in the latter paper. In summary, this described the frond as having a major dichotomy near its base, each resulting branch being tripinnate or rarely bipinnate. Pinnae (monopinnate or bipinnate) and/or large, orbicular cyclopterid pinnules may be attached to the primary rachis below the dichotomy. Intercalated, usually monopinnate pinnae are attached to the primary racheis between the secondary pinnae. Pinnae of all orders are terminated by a single apical pinnule.

This diagnosis contains a number of variable features, i.e. the degree of pinnation of the primary branches, the division of the intercalated elements, the presence or absence of pinnae below the main dichotomy, the presence or absence of cyclopterid pinnules. This might simply reflect variation within a 'natural' form-genus (*sensu* Cleal 1986), but may alternatively indicate that it is still an essentially artificial concept. It is hoped that evidence provided by the cuticles might help resolve this problem.

The suprageneric classification of Meyen (1987) is used here: *Neuropteris* is included within the order Trigonocarpales (syn. Medullosales *auct*). Even before the pteridosperms were recognized as gymnosperms, the medullosan affinities of *Neuropteris* had been suggested by Renault (1876) and Grand'Eury (1877), based on an analogy between the longitudinal striae on their rachides and the vascular segments of *Myeloxylon*. Despite the caution urged by Stidd (1981), the evidence from permineralized specimens seems to support the assumption (Reihman and Schabilion 1978; Oestry-Stidd 1979; Beeler 1982, 1983). The available evidence of *Neuropteris* fructifications is equivocal on this point (Stidd 1981). The families for presumed trigonocarpalean foliage proposed by Corsin (1960) have not been used here since they are based almost exclusively on sterile characters and are thus of doubtful validity. Instead, *Neuropteris* is regarded as a satellite form-genus within the order Trigonocarpales.

Neuropteris rarinervis Bunbury (1847)

Plate 97; text-figs. 4 and 5

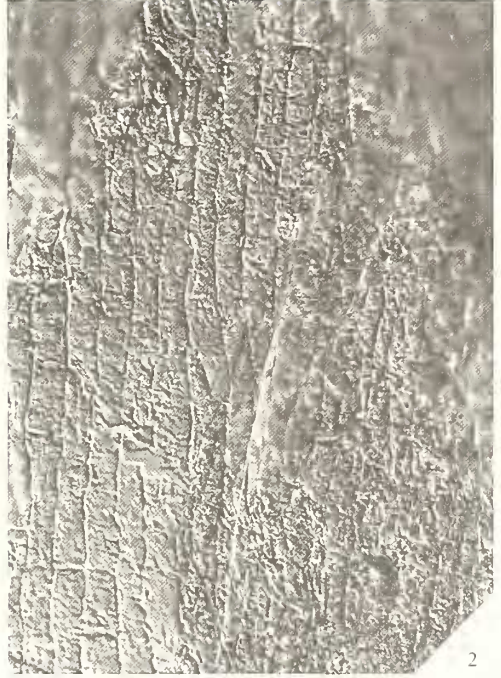| 1847 | *Neuropteris rarinervis* Bunbury, p. 425, pl. 22. |
1933	*Neuropteris attenuata* Lindley and Hutton; Stockmans (*non* Lindley and Hutton), p. 20, pl. 5.
1938	*Neuropteris rarinervis* Bunbury; Bell, p. 58, pl. 52, fig. 3; pl. 53, figs. 1 and 2; pl. 54, fig. 4.
1959	*Neuropteris rarinervis* Bunbury; Crookall, p. 122, pl. 30; pl. 31, figs. 1–3.
1967	*Neuropteris rarinervis* Bunbury; Laveine, p. 180, pls. 40–47.
1980*a*	*Neuropteris rarinervis* Bunbury; Zodrow and McCandlish, p. 45, pls. 34–36; pl. 37, fig. 1.
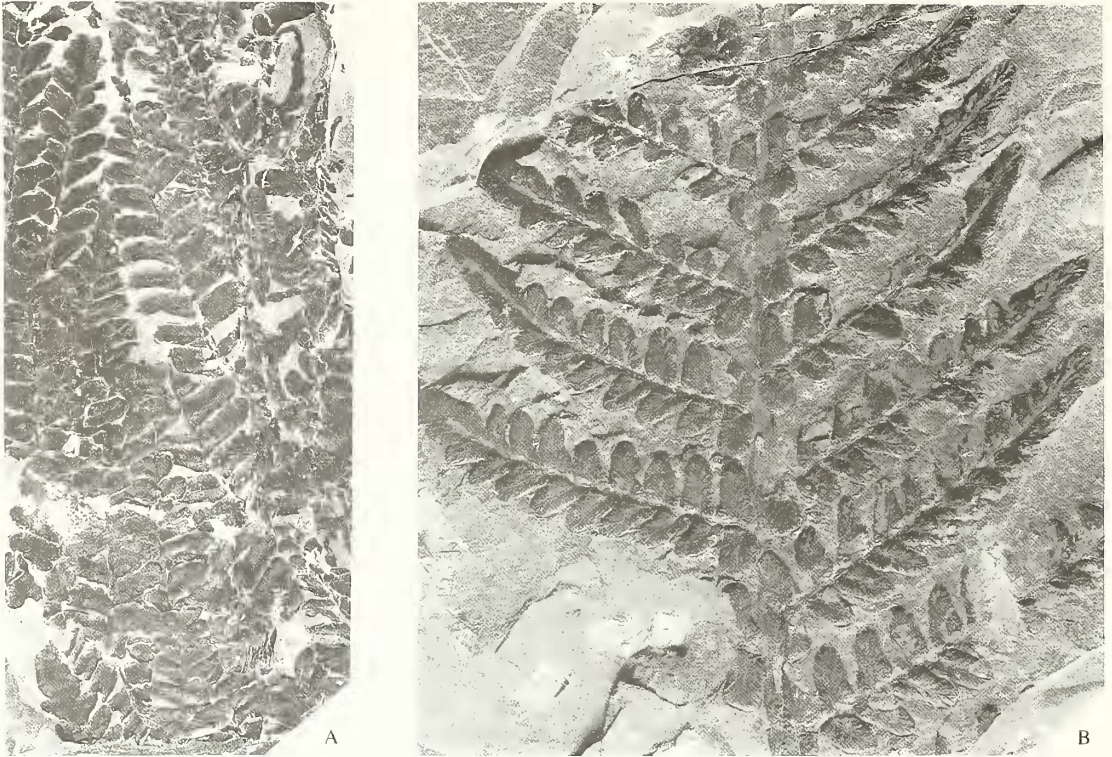
TEXT-FIG. 4. *Neuropteris rarinervis* Bunbury. Hand-specimens from which cuticles were prepared, Brogan's Pit, near Point Aconi, Sydney Coalfield, above Lloyd Cove Seam, Morien Group (upper Westphalian D). 4A, 982GF-274; × 1. 4B, 982GF-275; × 1·5.

Gross morphology. Pinnate foliage bears small, linguaeform lateral pinnules, 3–9 mm long and 1·5–3·5 mm wide (text-fig. 4). The pinnules are thick-limbed, often showing a prominent compression border. Pinnule base is semi-cordate except high in the pinna, and often has a prominent basiscopic and sometimes an acroscopic auricle. The auricles are usually large relative to the whole pinnule, importing a somewhat undulate margin to the pinnule. High in the pinna, pinnules become more broadly attached to the rachis and have straighter lateral margins. Pinnule apex is almost invariably broadly round. The catadromic pinnule of each ultimate pinna is often shorter and rounder than its neighbours. Midvein is prominent and slightly flexuous, extending for much of pinnule length. Lateral veins lie at 20–30° to midvein. In larger pinnules they arch, meeting the pinnule margin at 70–80°; in smaller pinnules they are straighter and may meet pinnule margin at *c*. 45°. Lateral veins are thick and generally fork once or twice at a wide angle, producing nervation density 18–25 veins per cm on pinnule margin. Racheis are longitudinally striate. Apical pinnules slender and somewhat trapezoidal in shape.

EXPLANATION OF PLATE 97

Figs. 1–4. *Neuropteris rarinervis* Bunbury. Cuticles photographed using Nomarski Contrast microscopy (except Fig. 3 using unpolarized light), Brogan's Pit, near Point Aconi, Sydney Coalfield, above Lloyd Cove Seam, Morien Group (upper Westphalian D). 1, CCB/982GF-274/11; cuticle from adaxial surface of pinnule, × 125. 2, CCB/982GF-274/11; cuticle from rachis, × 125. 3, CCB/982GF-274/8; general view of abaxial cuticle showing bands of stomata in intercostal fields, × 50. 4, CCB/982GF-274/8; close-up of stomata from abaxial cuticle, × 500.

PLATE 97

CLEAL and ZODROW, *Neuropteris*
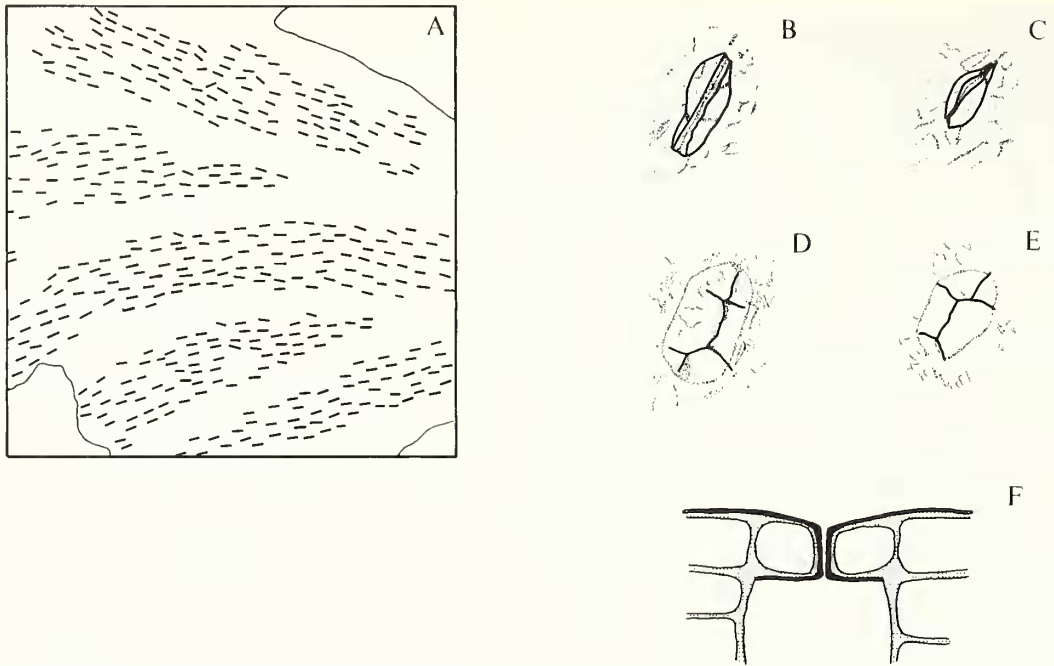
TEXT-FIG. 5. *Neuropteris rarinervis* Bunbury. Brogan's Pit, near Point Aconi, Sydney Coalfield, above Lloyd Cove Seam, Morien Group (upper Westphalian D). 5A, CCB/982GF-274/8; general view of abaxial cuticle showing distribution and orientation of stomata, each stomatal polar axis being represented by a black line, × 35. 5B, C, CCB/982GF-274/15; close-up of stomatal apparatus, as viewed from inner surface of cuticle, × 500. 5D, E, CCB/982GF-274/14; close-up of stomatal apparatus, as viewed from outer surface of cuticle, × 500. 5F, reconstruction of stomatal apparatus prior to fossilization, thick black lines representing cutinized surfaces.

Epidermal structure. Adaxial cuticle appears thick and brittle, with weakly developed intercellular flanges (Pl. 97, fig. 1), and weakly differentiated cell structure between intercostal and costal fields. The cells are irregularly subrectangular to polygonal, with long axes parallel to veins, up to 300 μm long and 35 μm wide. Intercostal cell walls are shallowly sinuous, with 'U'-shaped waves (wavelength 2–3 times amplitude). Costal cell walls are more shallowly sinuous, with 'U'-shaped waves (wavelength 3–4 times amplitude).

Abaxial cuticles are much thinner, showing little evidence of epidermal structure (Pl. 97, fig. 3). Some show a faint impression of cell walls in the costal fields. Costal cells are elongate, subrectangular to subrhomboidal, up to 180 μm long and 25 μm wide. Sparsely distributed trichome bases occur mainly in the costal fields (only rarely in the intercostal fields), 20–30 μm in diameter (Pl. 97, fig. 3). Stomatal guard cells occur in shallow depressions in the intercostal fields (text-fig. 5F). They are 20–30 μm long and 5 μm wide (Pl. 97, fig. 4) and lie below the surface of the cuticle (text-fig. 5B–F). Their polar axes are approximately parallel to the veins. Stomata are probably anomocytic, but this cannot be seen in the cuticle. Stomatal Index could not be determined.

Rachial cuticles are relatively thick, showing elongate subrectangular epidermal cells, longitudinally arranged (Pl. 97, fig. 2). Cells are 100 μm long and 15–30 μm wide. No rachial trichome bases were observed.

Remarks. Some authors (e.g. Stockmans 1933) have argued that *Neuropteris attenuata* Lindley and Hutton should take precedence over *N. rarinervis* Bunbury, ignoring the comment by Kidston (1886, p. 102) that the holotype of the latter is in fact a pecopterid, probably allied to *P. bucklandii* Brongniart (see also Laveine 1967). The Sydney Coalfield, from where all the specimens described in this paper originated, is the type area for *N. rarinervis* Bunbury.

The cordate base of the pinnules, the prominent midvein and non-anastomosed lateral veins

clearly correspond with the diagnosis of *Neuropteris*. Known details of the frond architecture also support its inclusion here. The specimens figured by Carpentier (1930, pl. 8) and Laveine (1967, pl. 45, fig. 3) show that the frond had a dichotomy producing tripinnate branches and large cyclopterid pinnules attached near the base. Specimens figured by Laveine (1967, pl. 42, fig. 1; pl. 43) show that intercalated pinnae were borne on antepenultimate racheis.

Compression fossils of this species show the pinnules to have been coriaceous, which is reflected in the thick and brittle adaxial cuticle (Pl. 97, fig. 1). The only other *Neuropteris* frond-type with such a thick cuticle is *N. ovata* var. *acoiiensis* nov. var. On present evidence, this feature seems to have no taxonomic significance.

As with some other neuropterids (*N. tenuifolia* Sternberg – Barthel 1962; *N. loshii* Brongniart – Daber 1963), the abaxial cuticle is too thin to show full details of the stomatal structure, particularly whether subsidiary cells are present (Pl. 97, fig. 4). The only significant details observed were that the stomata occur in shallow depressions (text-fig. 5F) and that the guard-cells were only clearly visible on the inner surface of the cuticle (contrast text-fig 5B, C with text-fig. 5D, E). The permineralized specimens described by Oestry-Stidd (1979) show that the stomata are anomocytic. The sinuous walls of the adaxial cells are also confirmed by Oestry-Stidd's study.

Neuropteris ovata Hoffmann *in* Keferstein (1826) var. *simonii* (Bertrand) comb. nov.

Plates 98 and 99; text-figs. 6–8, 11A

1915   *Neuropteris ovata* Hoffmann; Gothan, p. 377, pl. 32, figs. 1–4 (cuticles).
1925   *Cyclopteris* sp.; Florin, p. 231, pl. 10, figs. 3–12 (cuticles).
1930   *Mixoneura simoni* Bertrand, p. 45, pl. 29, figs. 1–4.
1941   Farnblatt; Guthörl, p. 250, text-fig. 8 (cuticle).
1962   *Neuropteris ovata* Hoffmann; Barthel, p. 24, pls. 18 and 19; pl. 20, figs. 1–3, 5 (cuticles).
1967   *Neuropteris ovata* Hoffmann; Laveine, p. 231, pls. 66 and 67.
1975   *Neuropteris ovata* Hoffmann; Doubinger and Germer (*pars*), p. 5, pl. 2, fig. 3.
1975   *Neuropteris pilosa* Doubinger and Germer, p. 18, pl. 7, fig. 1.
1975   *Neuropteris obliqua* (Brongniart); Doubinger and Germer (*non* Brongniart) (*pars*), pl. 3, fig. 2.
1980a   *Neuropteris* (*Mixoneura*) *ovata* Hoffmann; Zodrow and McCandlish, p. 44, pl. 28, fig. 3; pls. 29–32; pl. 33, fig. 1.
1983   *Neuropteris ovata* Hoffmann; Beeler, p. 2360, figs. 8, 18, 20–27.

Gross morphology. Pinnate foliage bears mainly subrectangular to ovoid pinnules, with a broadly round apex and a non-cordate base (Pl. 98, figs. 1 and 2; text-figs. 6 and 11A). These pinnules are 5–15 mm long and 3–10 mm wide, with a mean length:breadth ratio of *c.* 2·0. Rarely, larger subrectangular pinnules occur, up to 20 mm long, probably originating from intercalated pinnae low in the frond. Most pinnules show a basiscopic auricle (text-fig. 11A). Except in the largest pinnules, the midvein is strongly decurrent, extends for only half or less of the pinnule length. Vein density averages 35–43 veins per cm on the pinnule margin. The pinnae have a relatively small, ovoid apical pinnule, usually 5–14 mm long.

Epidermal structure. Adaxial epidermal structure is differentiated between intercostal and costal fields. Intercostal cells are subrectangular to polygonal, with long axes parallel to veins, 30–80 μm long and 20–45 μm wide (Pl. 99, fig. 2). Cell walls are markedly sinuous (wave-length twice amplitude), with 'U' or 'Ω' shaped waves. Costal cells are more consistently subrectangular and elongate, up to 200 μm long and 15–25 μm wide (Pl. 99, fig. 1). Along narrower veins, cell walls are sinuous, as in intercostal cells; but are straighter along broader veins. No trichomes are present.

Abaxial epidermal structure is differentiated between intercostal and costal fields (text-fig. 7A). Intercostal cells are irregularly polygonal with gently curved walls, 30–120 μm in size (Pl. 99, fig. 4; text-fig. 7A, B). Costal cells are more subrectangular and elongate, up to 250 μm long and 10–25 μm wide. Trichomes occur on costal fields and near pinnule margin (text-fig. 7A). In larger pinnules, trichomes also occur on intercostal fields. Trichomes are multicellular files, each cell *c.* 40 μm long, with no marked constriction at nodes. The most complete trichome fragments found are 550 μm long and 30 μm wide. Stomata are distributed throughout intercostal fields, with polar axes approximately parallel to veins (text-fig. 8A) and occur in shallow depressions on the cuticle (text-fig. 8F). Guard cells are 15–30 μm long and 2–5 μm wide and lie below the surface of the

TEXT-FIG. 6. *Neuropteris ovata* var. *simonii* (Bertrand). 979GF-230. Prince Mine, Sydney Mines, Sydney Coalfield, Morien group (exact horizon not recorded), Westphalian D, × 1·5.

cuticle (text-fig. 8F). Stomata are often anomocytic (Pl. 99, fig. 4), but there is sometimes a pair of weakly differentiated, lateral subsidiary cells in a brachyparacytic arrangement (text-fig. 7C). Stomatal Index varies from 30 to 35.

Rachial cuticles are relatively brittle, showing isodiametric, subrectangular epidermal cells in longitudinal rows (text-fig. 7D). Cells are 30–100 μm in size, depending on size of rachis. Trichome bases are present near where the pinnules are attached, 20–40 μm in diameter.

Remarks. Crookall (1959), Wagner (1963) and Laveine (1967) have extensively discussed the taxonomy of *N. ovata* Hoffmann. The form and nervation of the pinnules appear to correspond essentially to that of *Neuropteris*. Specimens described by Zodrow and Cleal (1988) indicated that its frond had the characteristic basal dichotomy producing tripinnate branches, with intercalated pinnae on the antepenultimate racheis. The only apparent discrepancy is the absence of large

EXPLANATION OF PLATE 98

Figs. 1 and 2. *Neuropteris ovata* var. *simonii* (Bertrand). 1, C/4723; fragment of typical ultimate pinna with small apical pinnule, Göttelborn Colliery, near Friedrichsthal, Saarland, Obere Kohlbach Seam, Heiligenwald Formation, lower Westphalian D, × 3. 2, 982GF-405; Point Aconi, Sydney Coalfield, about 1 m above Point Aconi Seam, Morien Group (lower Cantabrian), × 1.

PLATE 98
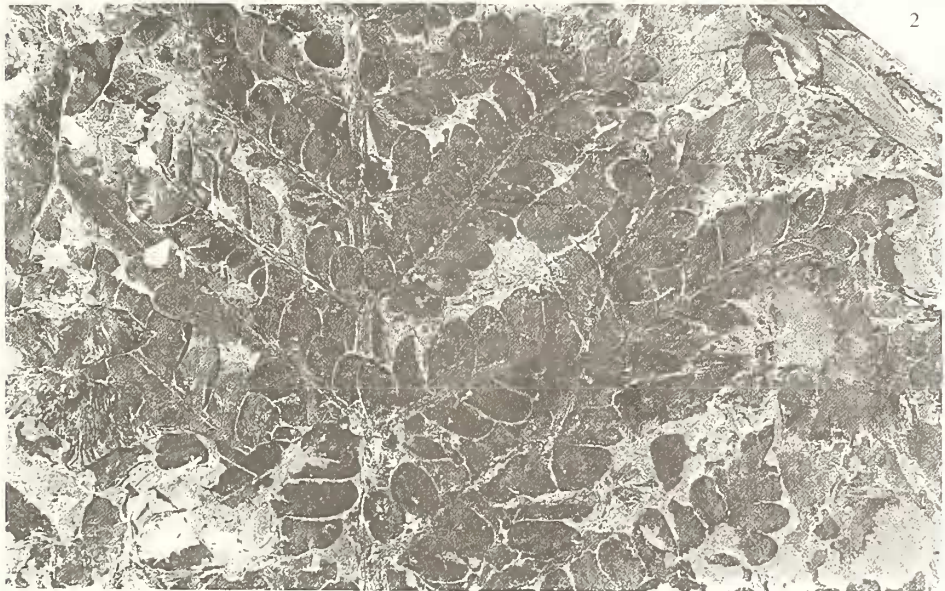
CLEAL and ZODROW, *Neuropteris*

cyclopterid pinnules attached directly to the main rachis near the base of the frond, and their replacement by short pinnae bearing fimbriate pinnules.

Cuticles similar to those found in this study have been previously described by Gothan (1915), Florin (1925), Guthörl (1941) and Barthel (1962), based on specimens from Saarland. The present study has revealed similar material from the Sydney Coalfield. It is widely assumed that it is the epidermal pattern of typical *N. ovata* Hoffmann, but the types of that species (from the Piesberg Coalfield, Germany – Hoffman *in* Keferstein 1826; Saltwedel 1968, 1969) are of too high a rank of coalification for the preservation of cuticles.

The type *N. ovata* Hoffmann, as re-described by Saltzwedel (1968, 1969), differs in several gross-morphological features from these Saarland and Sydney specimens. In particular, the type *N. ovata* Hoffmann has a higher vein density along the pinnule margin (mean *c.* 50 veins per cm) and a lower length:breadth ratio (*c.* 1·6). The apical pinnules also tend to be larger, being rarely less than 15 mm long.

Saltzwedel (1968) assigned all *N. ovata* Hoffmann specimens from the Westphalian of Saarland to var. *sarana*. It is shown below that *N. ovata* var. *sarana* should be restricted to the specimens from the upper Westphalian D of Saarland. We instead use the name *N. ovata* var. *simonii* for the lower and middle Westphalian D specimens, based on a comparison with the gross morphology of the types of *Mixoneura simonii* Bertrand (Bertrand 1930; Laveine 1967) from Nord-Pas-de-Calais coalfields. Saltwedel argued that these Nord-Pas-de-Calais specimens were indistinguishable from the *N. ovata* Hoffmann var. *ovata*; but this does not accord with our observations. Measurements taken from the Nord-Pas-de-Calais specimens showed a mean nervation density of *c.* 36 veins per cm, a mean pinnule length:breadth ratio of *c.* 1·9 and an apical pinnule length rarely greater than 15 mm. These characters clearly lie much nearer to the specimens described here than to the types of *N. ovata* Hoffmann var. *ovata*, but it must be recognized that the Nord-Pas-de-Calais specimens are unsuitable for cuticle preparations, and it is thus impossible to confirm this assumption based on epidermal characters.

We have assigned these variations on the *ovata* theme to separate varieties rather than species. The differences in gross morphology are relatively minor and epidermal structures are the only reliable means of distinguishing the variants. In this particular case, *simonii* has not previously been used at the rank of variety, nor has it ever been included within the form-genus *Neuropteris* (Bertrand (1930) referred to it as *Mixoneura simonii*). The new combination of *N. ovata* var. *simonii* (Bertrand) is thus proposed here.

The epidermal structures described by Beeler (1983) from permineralized specimens have many features in common with *N. ovata* var. *simonii* (Bertrand). In particular, the adaxial cells walls are sinuous, and the stomata are anomocytic and orientated approximately (but not consistently) parallel to veins. The only apparent difference is the absence of trichomes in the permineralized specimens, but this may be a taphonomic effect. This similarity is of interest because Beeler's material originated from an horizon high in the Conemaughian 'Series', which is probably near the Stephanian A-Stephanian B boundary in the west European chronostratigraphy (Phillips 1981). This is a higher horizon than usually yields *N. ovata* Hoffmann, although Wagner (1984) has shown

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EXPLANATION OF PLATE 99

Figs. 1–4. *Neuropteris ovata* var. *simonii* (Bertrand). Cuticles photographed using Nomarski Contrast microscopy. 1, V.62923; cuticle from adaxial surface of pinnule showing cells with sinuous walls, Itzenplitz Colliery, near Friedrichsthal, Saarland, Kallenberg Seam, Luisenthal Formation, lower Westphalian D, × 250. 2, CCB/982GF-405/6; cuticle from adaxial surface of pinnule, Point Aconi, Sydney Coalfield, about 1 m above Point Aconi Seam, Morien Group (lower Cantabrian), × 250. 3, CCB/979GF-230/3; cuticle from abaxial surface of pinnule, Prince Mine, Sydney Mines, Sydney Coalfield, Morien Group (exact horizon not recorded), Westphalian D, × 250. 4, CCB/979GF-230/1; cuticle from abaxial surface of pinnule, showing both stomata and trichome base, Prince Mine, Sydney Mines, Sydney Coalfield, Morien Group (exact horizon not recorded), Westphalian D, × 250.
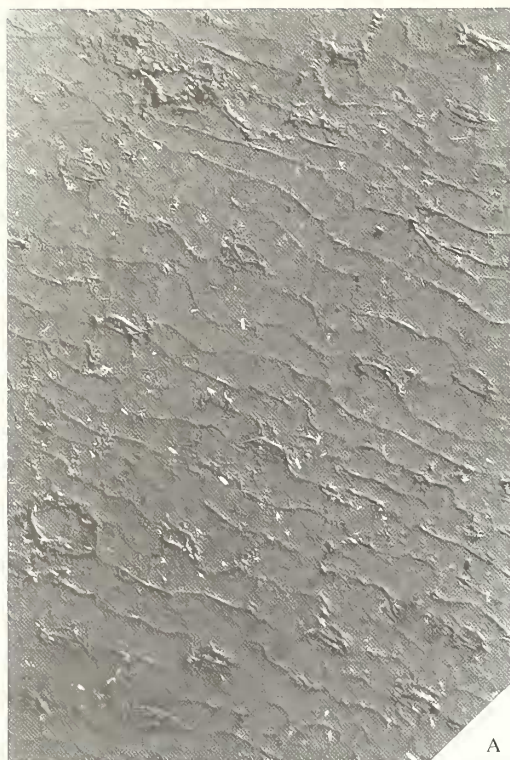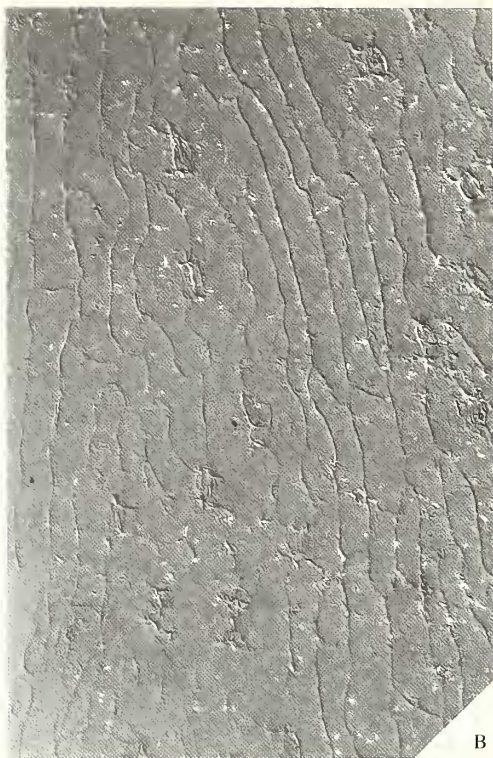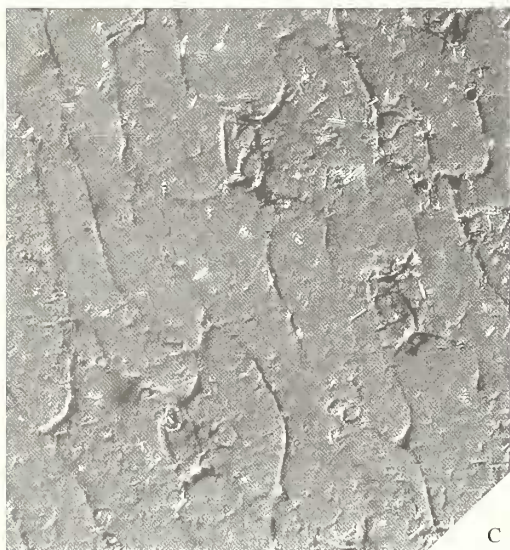
PLATE 99

CLEAL and ZODROW, *Neuropteris*

TEXT-FIG. 7. *Neuropteris ovata* var. *simonii* (Bertrand). Cuticles photographed using Nomarski Contrast microscopy, all specimens from Itzenplitz Colliery, near Friedrichsthal, Saarland, Kallenberg Seam, Luisenthal Formation, lower Westphalian D, except 7D, from Prince Mine, Sydney Mines, Sydney Coalfield, Morien Group (exact horizon not recorded) Westphalian D. 7A, V.62925; cuticle from abaxial surface of pinnule showing intercostal field and two costal fields, ×250. 7B, V.62924; cuticle from abaxial surface of pinnule, ×250. 7C, V.62925; close-up of stomata, ×500. 7D, CCB/979GF-230/4; cuticle from rachis, ×250.
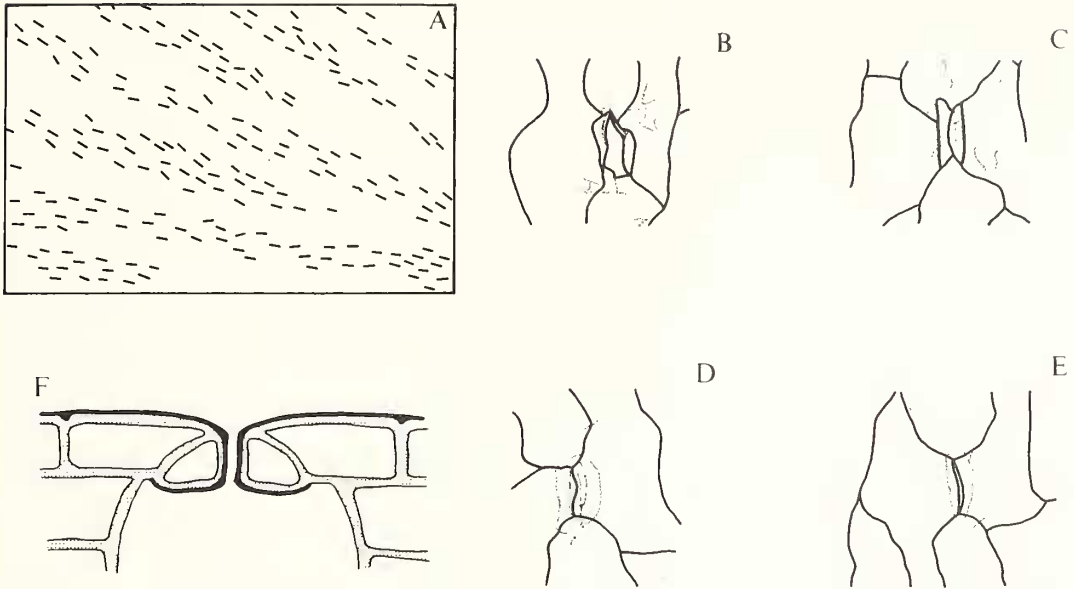
TEXT-FIG. 8. *Neuropteris ovata* var. *simonii* (Bertrand), Itzenplitz Colliery, near Friedrichsthal, Saarland, Kallenberg Seam, Luisenthal Formation, lower Westphalian D. 8A, V.62924; general view of abaxial cuticle showing distribution and orientation of stomata, each stomatal polar axis being represented by a black line, × 35. 8B, C, V.62925; close-up of stomatal apparatus, as viewed from inner surface of cuticle, × 500. 8D, E, V.62924; close-up of stomatal apparatus, as viewed from outer surface of cuticle, × 500. 8F, reconstruction of stomatal apparatus prior to fossilization, thick black lines representing cutinized surfaces.

it rarely to range up into the upper Stephanian. G. Rothwell (pers. comm., 1987) believes that they may belong to a different species from the Westphalian compression specimens described here, since no evidence of a basal dichotomy of the frond was found. This feature is only very rarely preserved and its absence in the permineralizations may just be a function of preservation.

The distinctive epidermal features of *N. ovata* var. *simonii* (Bertrand) are the strongly sinuous adaxial cells (Pl. 99, figs. 1 and 2), the anomocytic (rarely brachyparacytic) stomata distributed over the entire abaxial intercostal fields (Pl. 99, figs. 3 and 4; text-figs. 7A, B and 8), and the occurrence of multicellular files on both the costal and intercostal abaxial fields (Pl. 99, fig. 4; text-fig. 7B). The prominent intercellular flanges on the abaxial cuticle separate this species from the more 'typical' neuropterids, where they are absent or only weakly developed (e.g. *N. tenuifolia* Sternberg – Barthel 1962; *N. loshii* Brongniart – Daber 1963; *N. rarinervis* Bunbury – this study). Cuticles derived from cyclopteroid pinnules, associated with pinnate *N. ovata* var. *simonii* (Bertrand) foliage, show identical epidermal characters (Florin 1925, pl. 10, figs. 3–12). This is in marked contrast to the amphistomatic cyclopterids associated with *N. tenuifolia* Sternberg, whose epidermal characters are quite different from that of the pinnate foliage (Florin 1925, pl. 8, figs. 1–8, 11–12; pl. 9, figs. 1–6).

Neuropteris ovata Hoffmann *in* Keferstein (1826) var. *sarana* (Bertrand) comb. nov.

Plate 100; text-figs. 9 and 10

1926   *Mixoneura ovata* var. *sarana* Bertrand, p. 386.
1930   *Mixoneura sarana* Bertrand (*pars*), p. 36, pls. 19 and 20; pl. 20 bis, figs. 1–3; pl. 21.
1974   *Neuropteris ovata* Hoffmann; de Jong, p. 65, pl 24, fig. 2; pl. 26, figs. 1 and 2.
1975   *Neuropteris ovata* Hoffman; Doubinger and Germer, (*pars*), p. 5, pl. 1, figs. 3 and 4; pl. 2, figs. 1 and 2.
1975   *Mixoneura polyneura* Doubinger and Germer, p. 18, pl. 7, fig. 3.
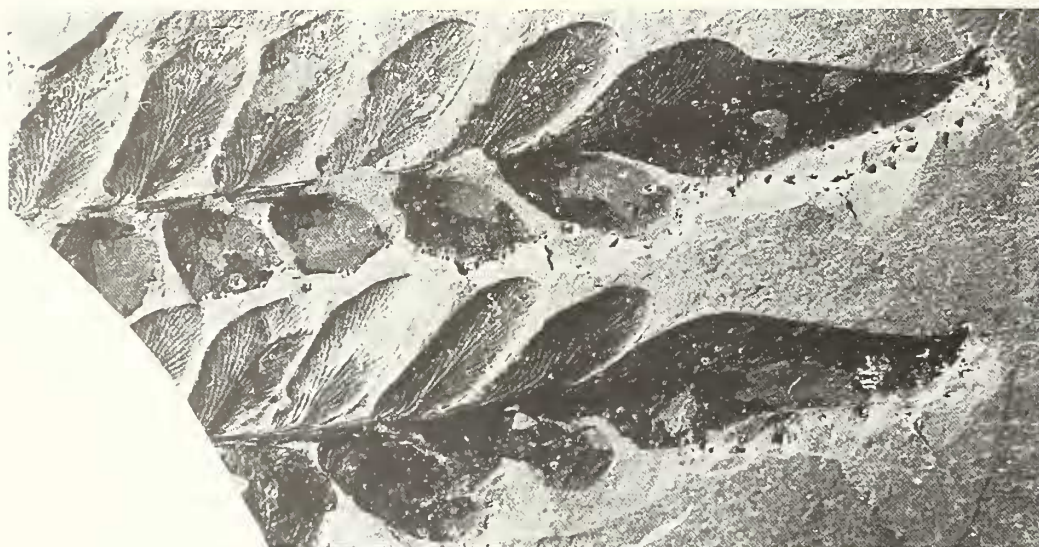
TEXT-FIG. 9. *Neuropteris ovata* var. *sarana* (Bertrand). C/5409. Fragments of typical pinnae showing larger apical pinnules than in var. *simonii*, Kohlwald Colliery, near Neunkirchen, Saarland, Huyssen Seam, Heiligenwald Formation, upper Westphalian D, × 3

Gross morphology. Pinnate foliage bears mainly subrectangular to ovoid pinnules, with a broadly round apex and a non-cordate base (text-fig. 9). Such pinnules are 5–15 mm long and 3–10 mm wide, with a mean length:breadth ratio of 1·9. Rarely, larger subrectangular pinnules occur, up to 20 mm long, probably originating from intercalated pinnae low in the frond. Most pinnules show a basiscopic auricle. Except in the largest pinnules, the midvein is strongly decurrent, and extends for only half or less of the pinnule length. Nervation density averages *c.* 40 veins per cm on the pinnule margin. The ultimate pinnae have a relatively large, subrhomboidal apical pinnule, usually 5–40 mm long.

Epidermal structure. Adaxial epidermal structure is differentiated between intercostal and costal fields. Intercostal cells are subrectangular to polygonal, with long axes parallel to veins, 60–120 μm and 30–60 μm wide (Pl. 100, fig. 1). Cell walls are markedly sinuous (wave-length twice amplitude), with 'U' or 'Ω' shaped waves. Costal cells are more consistently subrectangular and elongate, up to 200 μm long and 20–30 μm wide (Pl. 100, fig. 2). Along narrower veins, cell walls are sinuous, as in intercostal cells; but are straighter along broader veins. No trichomes are present.

Abaxial epidermal structure is differentiated between intercostal and costal fields. Intercostal cells are irregularly polygonal with gently curved walls, 30–75 μm in size (Pl. 100, fig. 3). Costal cells are more subrectangular and elongate, up to 150 μm long and 20–30 μm wide (Pl. 100, fig. 3). Trichome bases 50 μm in diameter occur on costal fields (Pl. 100, fig. 3), but no actual trichomes were found. Stomata (Pl. 100, fig. 4) occur in narrow bands between the veins, with polar axes approximately parallel to veins (text-fig. 10A). Guard cells are 18–30 μm long and 3–6 μm wide, and slightly raised above pinnule surface (text-fig. 10D). The stomata

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EXPLANATION OF PLATE 100

Figs. 1–4. *Neuropteris ovata* var. *sarana* (Bertrand). Cuticles photographed using Nomarski Contrast microscopy, Kohlwald Colliery, near Neunkirchen, Saarland, Huyssen Seam, Heiligenwald Formation, upper Westphalian D. 1, V.62938; cuticle from adaxial surface of pinnule showing intercostal field, × 250. 2, V.62938; cuticle from adaxial surface of pinnule showing costal field, × 250. 3, V.62939; cuticle from abaxial surface showing trichomes, and a row of stomata along intercostal field, × 250. 4, V.62937; close-up of stomatal apparatus, × 500.

PLATE 100

CLEAL and ZODROW, *Neuropteris*
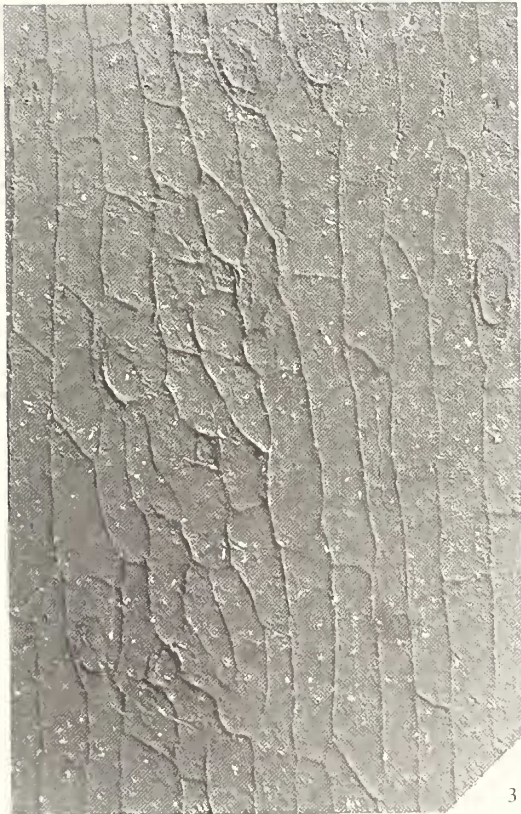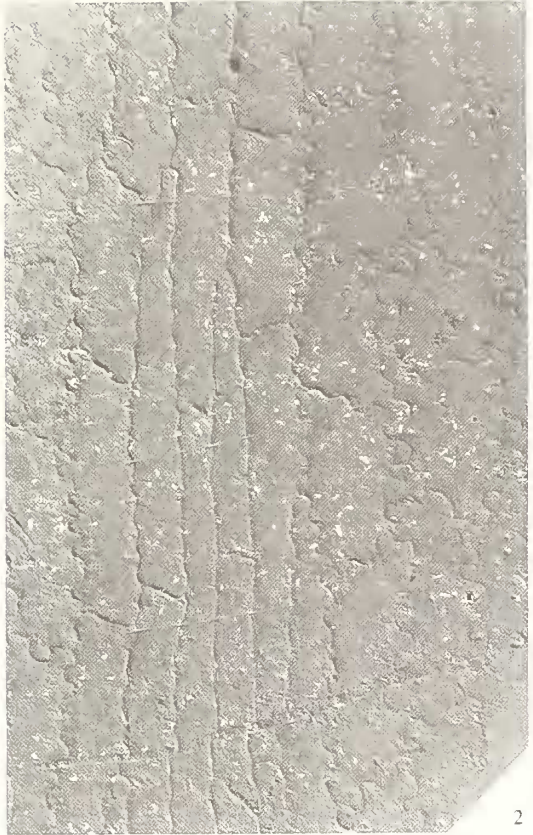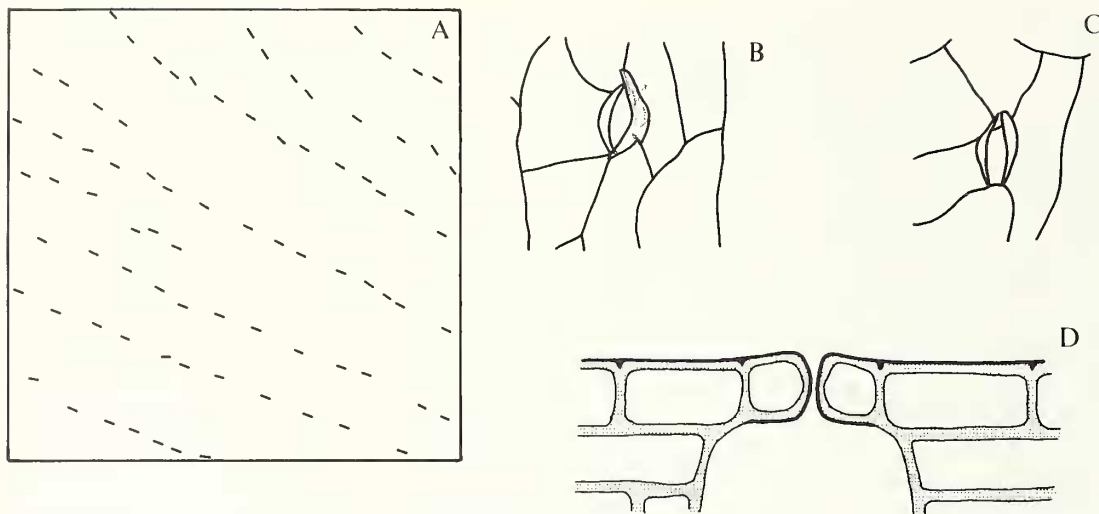
TEXT-FIG. 10. *Neuropteris ovata* var. *sarana* (Bertrand). Kohlwald Colliery, near Neunkirchen, Saarland, Huyssen Seam, Heiligenwald Formation, upper Westphalian D. 10A, V.62937; general view of abaxial cuticle showing distribution and orientation of stomata, each stomatal polar axis being represented by a black line, × 35. 10B, C, V.62937; close-up of stomatal apparatus, as viewed from inner surface of cuticle, × 500. 10D, reconstruction of stomatal apparatus prior to fossilization, thick black lines representing cutinized surfaces.

are rarely anomocytic, but more commonly brachyparacytic, with weakly differentiated subsidiary cells. Stomatal Index varies from 25 to 30.

Rachial cuticles are relatively brittle, showing isodiametric, subrectangular epidermal cells in longitudinal rows. Cells are 20–70 μm in size, depending on size of rachis. Trichome bases are *c.* 25 μm in diameter, and are distributed over the rachial surface. The rachial trichomes are gently tapered multicellular files, divided into 60–130 μm long segments. No complete rachial trichome was found, the largest fragment being 400 μm long.

Remarks. In Saarland, *N. ovata*-type fronds have a slightly different morphology in the upper Heiligenwald Formation, with distinctly larger, more rhomboidal apical pinnules (Cleal 1984*b*, p. 337). Examples of such specimens have been figured by Doubinger and Germer (1975). We assign them to *N. ovata* var. *sarana* Bertrand for two reasons. First, the type specimens originated from a similarly high stratigraphical horizon in the Saar–Lorraine Coalfield (Bertrand 1930); and second, these types show similarly large apical pinnules. Saltzwedel (1968) argued that *N. ovata* var. *sarana* occurred throughout the Westphalian D of Saar–Lorraine, but it is significant that most of the specimens examined by him from this coalfield came from the upper part of the stage. Both gross morphology and epidermal structure suggest that two varieties occur here: *N. ovata* var. *simonii* in the lower and middle Westphalian D, and *N. ovata* var. *sarana* in the upper Westphalian D.

The most obvious difference in epidermal structure between these specimens and *N. ovata* var. *simonii* (Bertrand) is that the stomata occur in single file along the middle of the intercostal fields (compare text-fig. 10A with text-fig. 8A respectively). The structure of the stomatal apparatus is essentially similar in the two varieties, except that the subsidiary cells are rather more strongly developed and the guard cells are slightly raised above the cuticle surface in *N. ovata* var. *sarana* (compare text-fig. 10D with text-fig. 8F).

Neuropteris ovata Hoffmann *in* Keferstein 1826, var. *aconiensis* var. nov.

Plate 101; text-figs. 11B and 12

Gross morphology. Pinnate foliage bears mainly subrectangular to ovoid pinnules, with a broadly round apex and a non-cordate base (text-fig. 11B). Such pinnules are 5–15 mm long and 3–10 mm wide, and have a basiscopic auricle. The midvein is strongly decurrent, and extends for only half or less of the pinnule length.
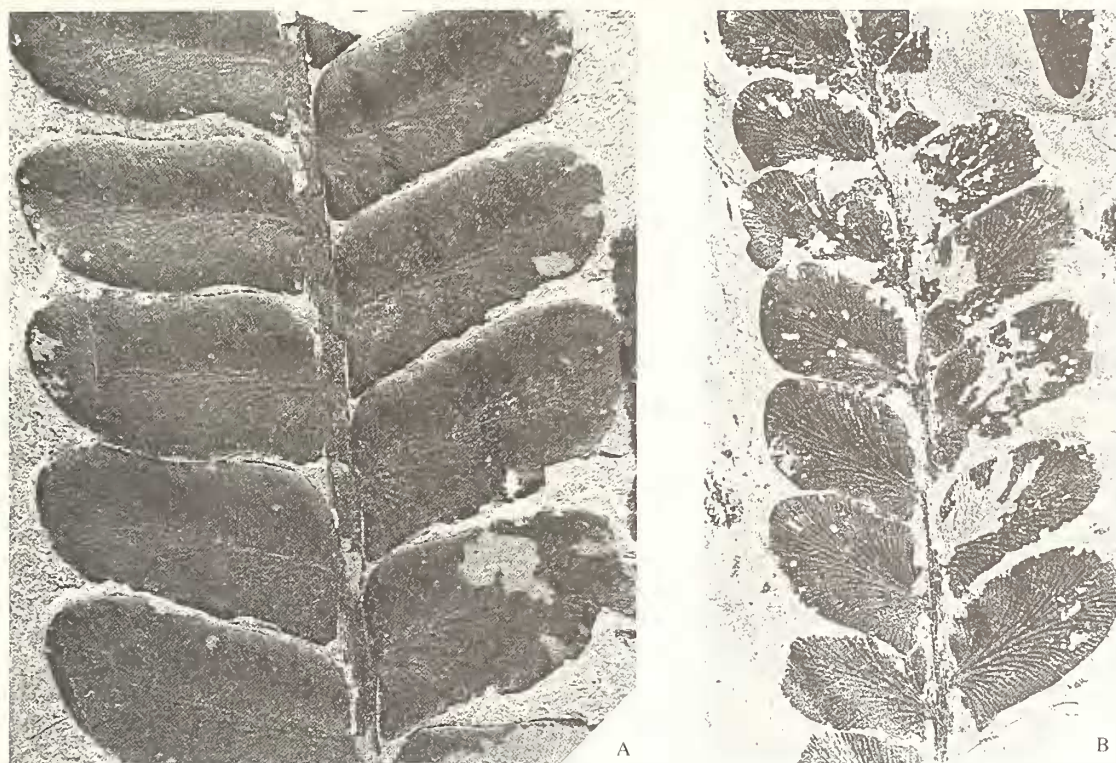
TEXT-FIG. 11A, *Neuropteris ovata* var. *simonii* (Bertrand). 977GF-126. Private drift mine 1 km west of Steele's Road, Glace Bay, Sydney Coalfield, Emery Seam, Morien group (middle Westphalian D), ×3. 11B. *Neuropteris ovata* var. *aconiensis* var. nov. 985GF-236. Point Aconi, Sydney Coalfield, Point Aconi Seam, Morien Group (lower Cantabrian), ×3.

The nervation density averages *c.* 40 veins per cm on the pinnule margin. The pinnae have a relatively small, ovoid apical pinnule, usually 5–12 mm long.

Epidermal structure. Adaxial cuticle is thick and brittle compared with that on the abaxial surface. Adaxial epidermal structure is weakly differentiated between intercostal and costal fields (Pl. 101, fig. 1). The cells are irregularly polygonal with straight walls, 20–60 μm in size (Pl. 101, fig. 2). No trichomes are present.

Abaxial epidermal structure is strongly differentiated between intercostal and costal fields (Pl. 101, fig. 3). Intercostal cells are irregularly polygonal with gently curved walls, 20–60 μm in size (Pl. 101, fig. 3). Costal cells are more subrectangular and elongate, up to 200 μm long and 15–40 μm wide (Pl. 101, fig. 3). Small anomocyctic stomata occur throughout intercostal fields, with polar axes approximately parallel to veins (text-fig. 12). Slightly sunken guard cells are 10–20 μm long and 3 μm wide (Pl. 101, figs. 4 and 5; text-fig. 12D). Stomatal Index varies from 17 to 19.

Remarks. These cuticles were prepared from a Point Aconi specimen, which seemed indistinguishable in gross morphology from *N. ovata* var. *simonii* (Bertrand), but had quite a distinct epidermal structure. To check that the discrepancy was not due to contamination, a second set of cuticles was prepared from the same specimen, but this confirmed the original results. *N. ovata* var. *simonii* (Bertrand) and *N. ovata* var. *aconiensis* var. nov. have several features in common, particularly the distribution of cells on the abaxial surface. Clear differences exist such as the thicker adaxial cuticle, the non-flexuous adaxial cell walls, the smaller stomata, lower Stomatal Index and the existence of papillae. The structures seen in this Point Aconi specimen may reflect xeromorphic adaptations, but the features used by Schabilion and Reihman (1985) to recognize sun-leaves (e.g. higher stomatal density) were not found.

Since it is indistinguishable from *N. ovata* var. *simonii* (Bertrand) using gross morphology, but has a clearly different epidermal structure, we propose to place it in a new variety, named *N. ovata* var. *aconiensis*, after the locality from where it originated.

Neuropteris flexuosa Sternberg (1825)

Plates 102 and 103; text-figs. 13 and 14

1823   *Osmunda gigantea* var. *β* Sternberg, p. 36, p. 39, pl. 32, fig. 2.
1825   *Neuropteris flexuosa* Sternberg, p. xvi.
1933   *Neuropteris tenuifolia* Sternberg; Stockmans (*pars*), p. 14, pl. 4, fig. 3.
1938   *Neuropteris (Mixoneura) flexuosa* Sternberg; Bell, p. 55, pl. 46, figs. 6 and 7; pl. 47, figs. 1–4; pl. 48, figs. 1 and 2.
1959   *Neuropteris ovata* Hoffmann forma *flexuosa* Sternberg; Crookall, p. 158, pl. 37, figs. 1–3; pl. 38, figs. 1–3; pl. 49, figs. 5–6; pl. 50, figs. 3–5.
1980*a*   *Neuropteris (Mixoneura) flexuosa* Sternberg; Zodrow and McCandlish (*pars*), p. 40, pl. 22, fig. 2; pls. 23 and 24.
1980*b*   *Neuropteris (Mixoneura) flexuosa* Sternberg; Zodrow and McCandlish, p. 57, pls. 1–4.

Gross morphology. Pinnate foliage bears relatively large, sub-oblong lateral pinnules, 1·2–2·5 cm long and 0·5–0·8 cm wide (text-fig. 13). Pinnule apex is round or bluntly acuminate. Pinnules are constricted at the base, usually non-cordate and basiscopically auriculate, except towards the pinna apex where they become broadly attached to the rachis. The midvein is thick, often basally decurrent in smaller pinnules, less so in larger pinnules. In fully developed pinnules, the midvein extends for up to three-quarters of the pinnule length, but less in smaller pinnules. Lateral veins are attached to midvein at low angle, but then broadly arch to meet pinnule margin at nearly right-angles. Lateral veins fork 2–4 times, and sometimes appear slightly flexuous. Nervation density is 32–40 veins per cm on pinnule margin. Ultimate racheis are coarsely striate, up to 2·5 mm wide. Apical pinnules are large and trapezoidal, up to 2 cm or more long and 1–1·5 cm wide (text-fig. 13A).

Epidermal structure. Adaxial epidermal structure is differentiated between intercostal and costal fields (Pl. 102, fig. 1). Intercostal cells are irregularly polygonal, with long axes parallel to veins, up to 200 μm long and 50 μm wide (Pl. 102, fig. 3). Cell walls are broadly curved. Costal cells are more consistently subrectangular and elongate with straighter walls, up to 200 μm long and 25 μm wide. No adaxial trichomes were found.
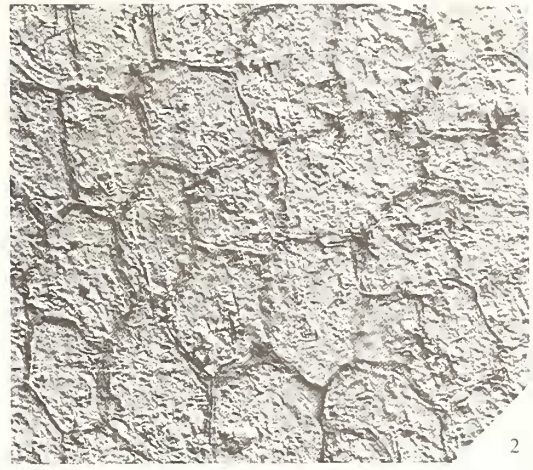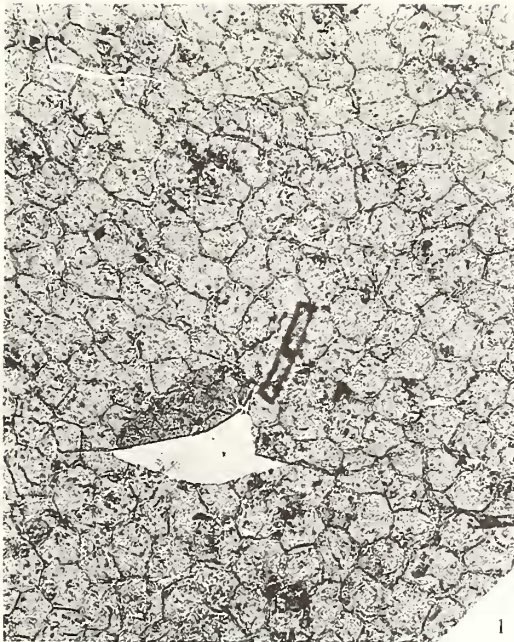
Abaxial epidermal structure is differentiated between intercostal and costal fields (Pl. 103, fig. 1). Intercostal cells are irregularly polygonal with gently curved walls, up to 100 μm in size (Pl. 103, fig. 2). Costal cells are more subrectangular and elongate, up to 150 μm long and 25 μm wide (Pl. 103, fig. 1). Small papillae occur in the centre of most abaxial cells (Pl. 103, fig. 3). Papillae are conoidal with a broadly round apex, *c.* 20 μm wide at base and 10–20 μm high. Larger tricomes occur on the costal fields (Pl. 103, fig. 1) and near pinnule margin (Pl. 102, fig. 4). In larger pinnules, trichomes also occur on intercostal fields. These larger trichomes are multicellular files, each cell *c.* 80 μm long, with a weak constriction at nodes. Most complete fragments of the multicellular files found are 500 μm long and 50 μm wide. Anomocyctic stomata are distributed throughout intercostal fields, with polar axes approximately parallel to veins (text-fig. 14A). Slightly sunken guard cells are 20–25 μm long and 5 μm wide (Pl. 103, fig. 4; text-fig. 14B–F). The papilla on each neighbouring cell surrounding the stomata occurs near the guard cells and tends to over-arch the pore. Stomatal Index varies from 15 to 18.
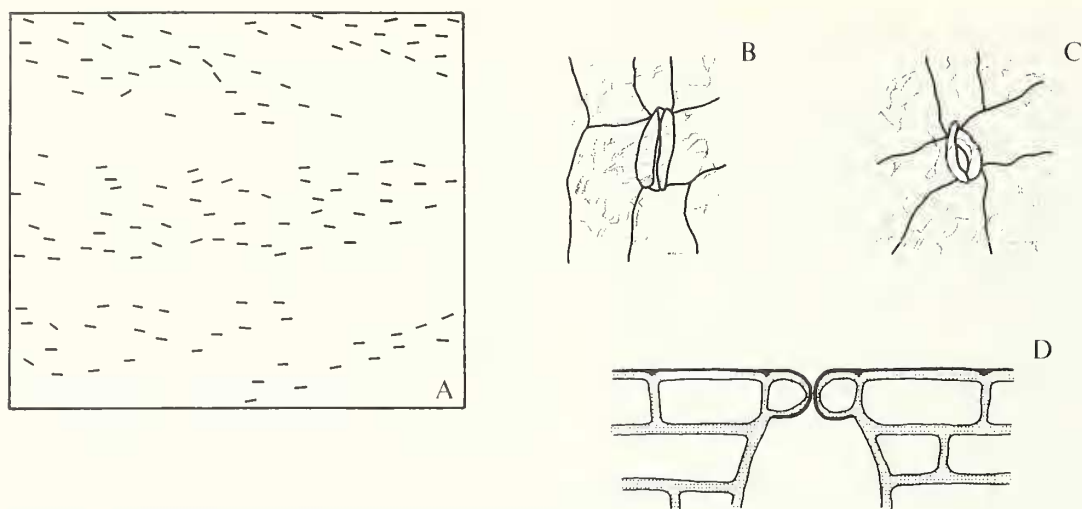
Rachial cuticles are relatively thick, showing isodiametric, subrectangular epidermal cells in longitudinal

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PLATE 101

CLEAL and ZODROW, *Neuropteris*

TEXT-FIG. 12. *Neuropteris ovata* var. *aconiensis* var. nov. Point Aconi, Sydney Coalfield, Point Aconi Seam, Morien Group (lower Cantabrian). 12A, CCB/985GF-236/10; general view of abaxial cuticle showing distribution and orientation of stomata, each stomatal polar axis being represented by a black line, × 35. 12B, C, CCB/985GF-236/14; close-up of stomatal apparatus, as viewed from inner surface of cuticle, × 500. 12D, reconstruction of stomatal apparatus prior to fossilization, thick black lines representing cutinized surfaces.

rows (Pl. 102, fig. 2). Cells are 20–50 μm in size, depending on size of rachis. Trichome bases are *c.* 60 μm in diameter and sparsely distributed along the rachis, but no trichomes were found.

Remarks. It has been argued that *N. flexuosa* Sternberg is closely related to *N. ovata* Hoffman (e.g. Crookall 1959). This is supported by the epidermal structures. The prominently developed intercellular flanges on the abaxial cuticle, the anomocytic structure of the stomatal apparatus and their restriction to the abaxial intercostal fields, and the presence of multicellular files mainly in the abaxial costal fields are features shared by both species. However, *N. flexuosa* Sternberg has several quite marked differences, particularly the presence of papillae on the abaxial surface, and the absence of strongly sinuous cell walls on the adaxial surface.

The epidermal evidence clearly rules out the suggestion of Stockmans (1933) that *N. flexuosa* Sternberg is a form of *N. tenuifolia* Sternberg. Barthel (1962) has shown that the latter has a very thin abaxial cuticle with much more slender multicellular trichomes and no evidence of papillae. The epidermal evidence also rules out de Jong's (1974) suggestion, that *N. macrophylla* Brongniart (described below) is a heterotypic synonym of *N. flexuosa* Sternberg.

EXPLANATION OF PLATE 102

Figs. 1–4. *Neuropteris flexuosa* Sternberg. Cuticles photographed using Nomarski Contrast microscopy (except Figs. 1 and 2 using unpolarized light). 1, CCB/977GF-267/2; cuticle from adaxial surface of pinnule, Prince Mine, Point Aconi, Sydney Coalfield, 5–25 cm above Hub Seam, Morien Group (upper Westphalian D), × 50. 2, CCB/981GF-354/2; cuticle from rachis, Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), × 50. 3, CCB/977GF-267/2; close-up of cuticle from adaxial surface of pinnule, Prince Mine, Point Aconi, Sydney Coalfield, 5–25 cm above Hub Seam, Morien Group (upper Westphalian D), × 125. 4, CCB/977GF-267/3, cuticle from edge of abaxial surface of pinnule showing numerous trichome bases, Prince Mine, Point Aconi, Sydney Coalfield, 5–25 cm above Hub Seam, Morien Group (upper Westphalian D), × 125.

PLATE 102

CLEAL and ZODROW, *Neuropteris*
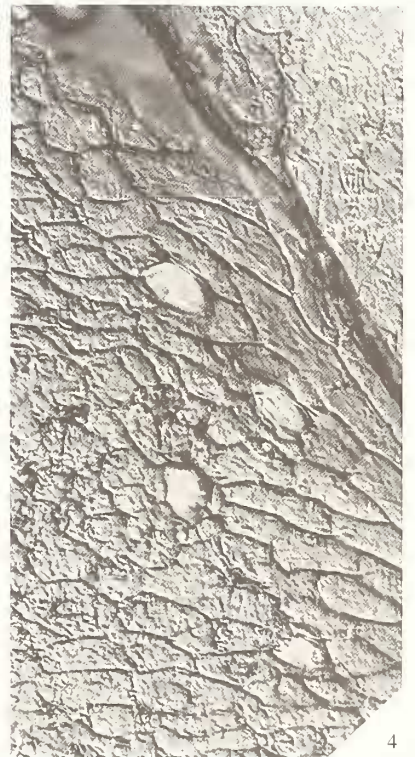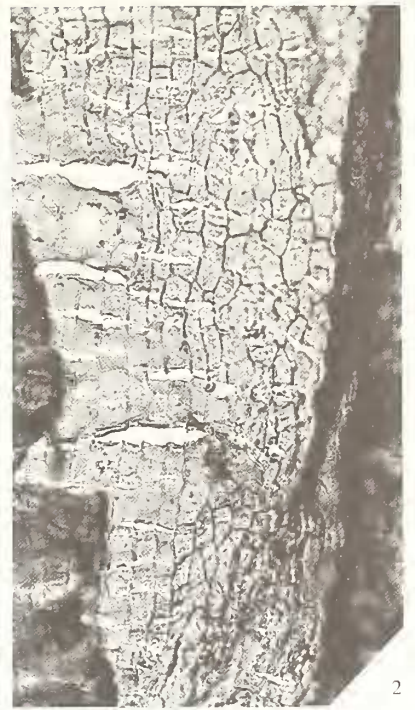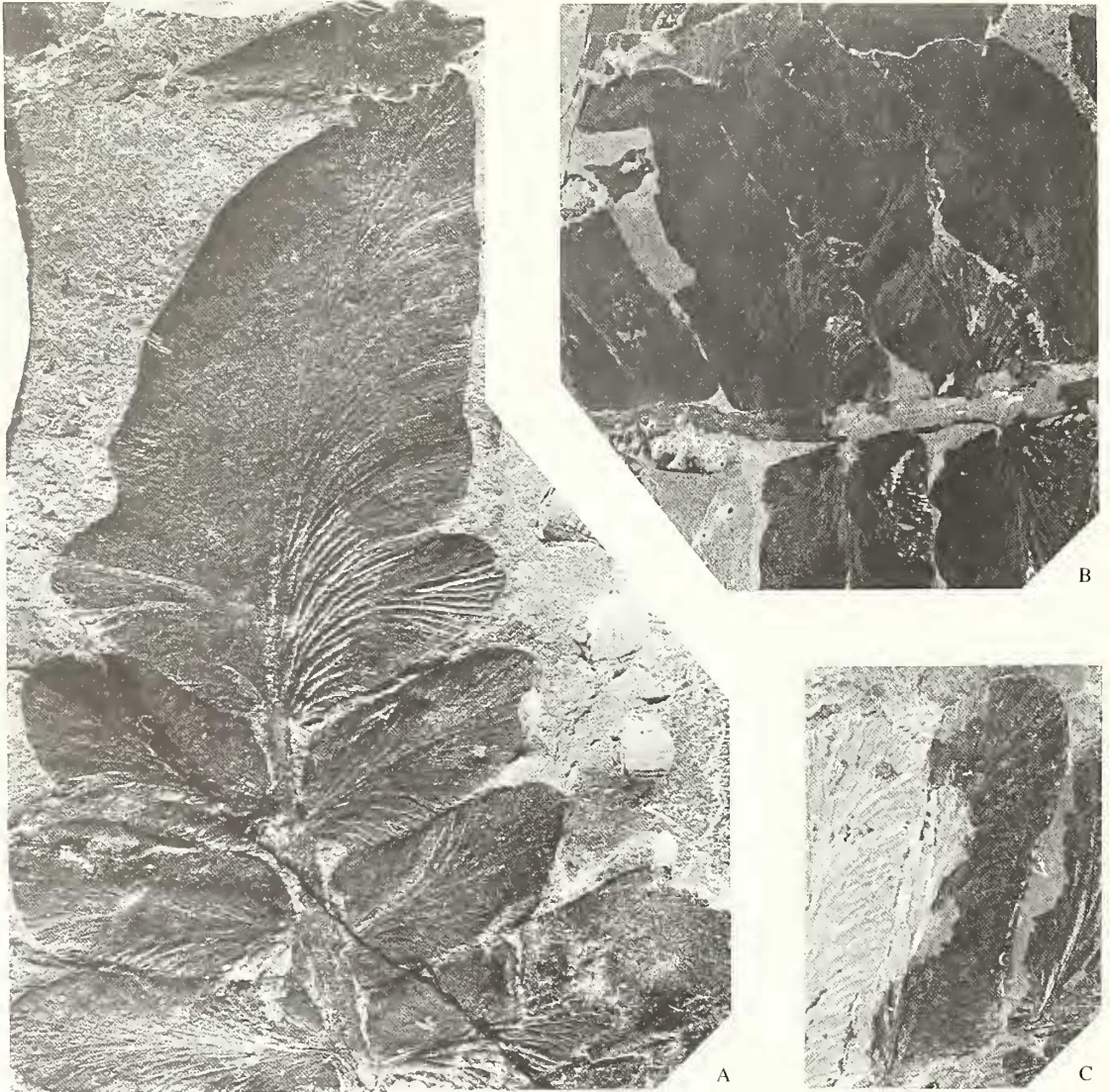
TEXT-FIG. 13. *Neuropteris flexuosa* Sternberg. 13A, 981GF-353; Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), ×3. 13B, 981GF-354; Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), ×3. 13C, 977GF-268; Prince Mine, Point Aconi, Sydney Coalfield, 5–25 cm above Hub Seam, Morien Group (upper Westphalian D), ×3.

Neuropteris macrophylla Brongniart (1831)

Plates 104 and 105; text-figs. 15 and 16

1831 *Neuropteris macrophylla* Brongniart, p. 235, pl. 65, figs. 1, 1a
1858 *Neuropteris Clarksoni* Lesquereux *in* Rogers, p. 857, pl. 6, figs. 1–4.
1879 *Neuropteris Clarksoni* Lesquereux; Lesquereux, p. 94, pl. 9, figs. 1–6.
1938 *Neuropteris macrophylla* Brongniart; Bell, p. 60, pl. 54, fig. 5; pl. 55, figs. 2–4.
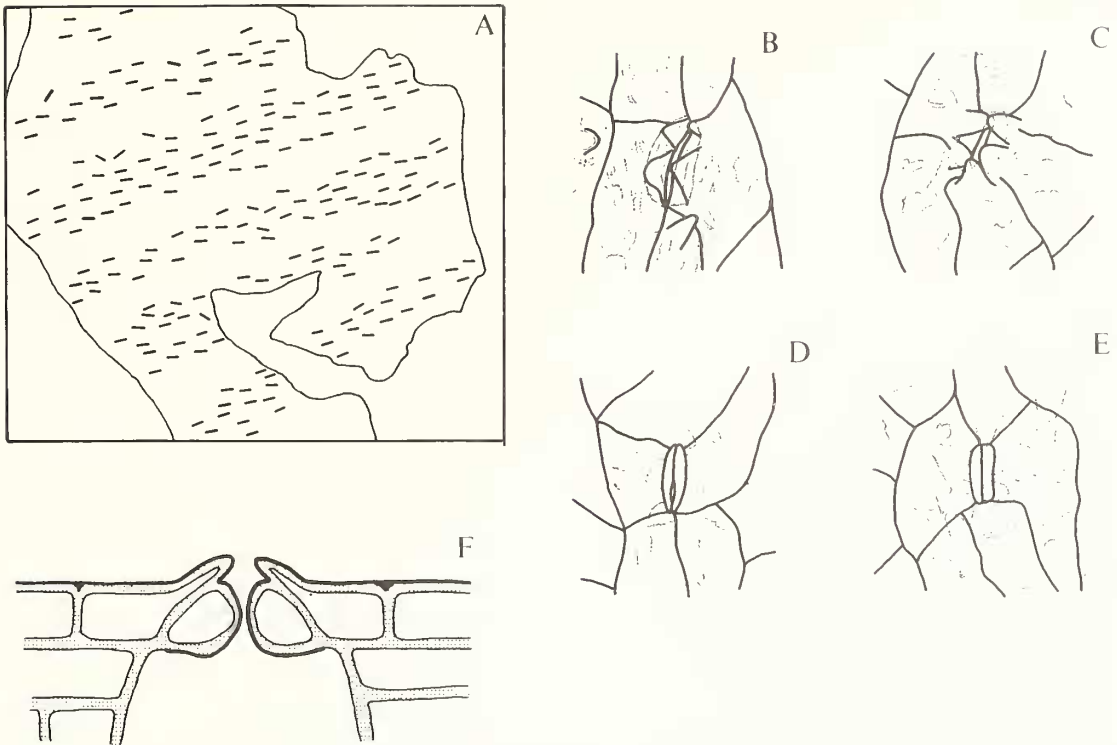1959 *Neuropteris macrophylla* Brongniart; Crookall, p. 176, pl. 38, fig. 4; pl. 39, fig. 1; pl. 40, figs. 1–3; pl. 42, figs. 1 and 3.

TEXT-FIG. 14. *Neuropteris flexuosa* Sternberg. Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D). 14*A*, CCB/981GF-353/3; general view of abaxial cuticle showing distribution and orientation of stomata, each stomatal polar axis being represented by a black line, × 35. 14B, CCB/981GF-353/6; close-up of stomatal apparatus, as viewed from inner surface of cuticle, × 500. 14C, CCB/981GF-353/3; close-up of stomatal apparatus, as viewed from inner surface of cuticle, × 500. 14D, E, CCB/981GF-354/8; close-up of stomatal apparatus, as viewed from outer surface of cuticle, × 500. 14F, reconstruction of stomatal apparatus prior to fossilization, thick black lines representing cutinized surfaces.

1980*a*   *Neuropteris macrophylla* Brongniart; Zodrow and McCandlish, p. 43, pl. 43, fig. 2.
1987   *Neuropteris macrophylla* Brongniart; Shute and Cleal, p. 555, fig. 2 (rachial cuticle).

Gross morphology. Pinnate foliage bears large, mainly subtriangular to sublanceolate pinnules up to 6·5 cm long (text-fig. 15). Smaller pinnules are more consistently subtriangular, with somewhat barrelled lateral margins. Except high in the pinna, pinnules have a strongly cordate base, with a very prominent basiscopic auricle. This auricle is often strongly developed, giving the pinnule a markedly asymmetrical aspect. The pinnules high in the pinna are usually more broadly attached to the rachis. The larger pinnules usually have an acuminate apex, the smaller pinnules sometimes a more round one. Midvein is thick and only slightly decurrent at base, extending for half to three quarters of pinnule length. Lateral veins lie at an acute angle to midvein, arch slightly and meet the pinnule margin at 60–80°. They fork up 6 times at a low angle, providing a nervation density of 34–40 veins per cm on pinnule margin. Fine punctae are often visible on veins and intercostal areas, probably due to abaxial epidermal papillae (see below). Racheis are longitudinally striate and sometimes show fine punctae. Apical pinnules of the pinnae are approximately lanceolate, often with an undulate margin.

Epidermal structure. Adaxial epidermal structure is differentiated between intercostal and costal fields (Pl. 104, fig. 1). Over most of the surface, cells are subrectangular to polygonal, fairly isodiametric, 40–60 μm in size. Along the midvein, cells are more consistently subrectangular and elongate, up to 160 μm long and 50 μm wide.
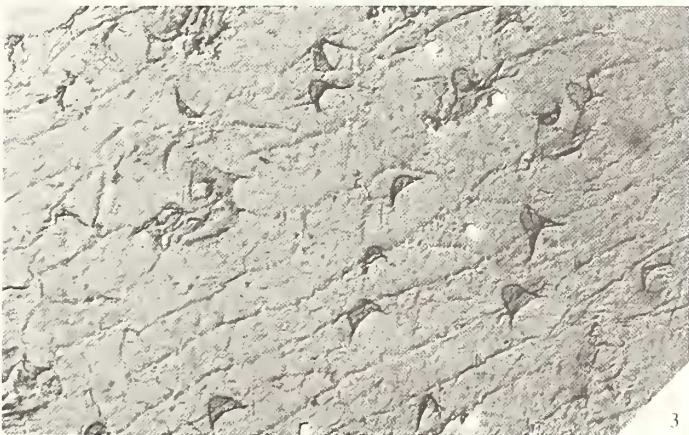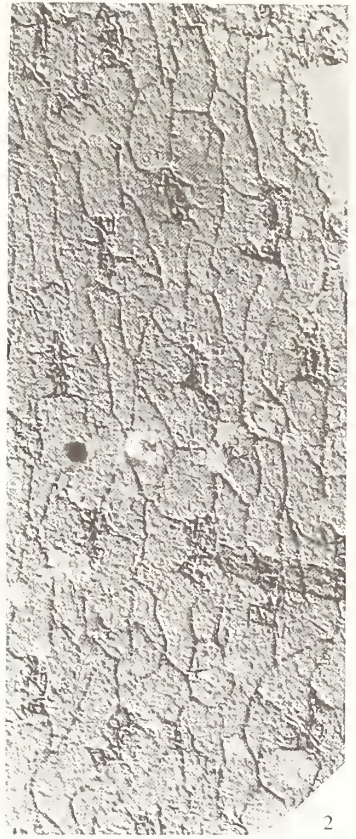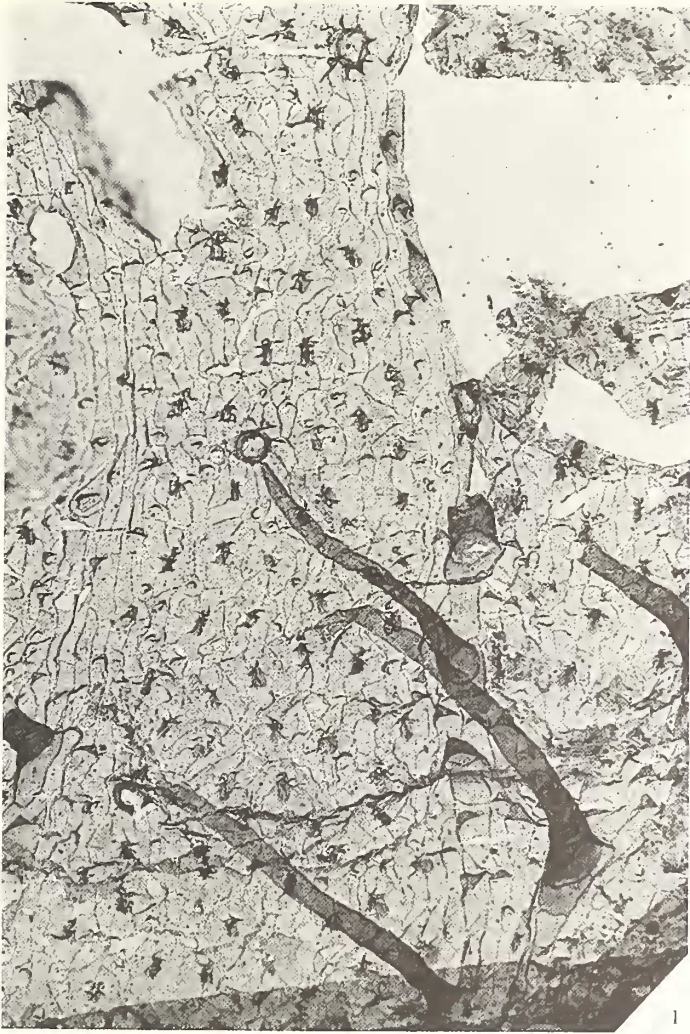
TEXT-FIG. 15. *Neuropteris macrophylla* Brongniart. 982GF-229. Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), × 1.

Abaxial cuticles are extremely thin and easily crumpled, but nevertheless preserve the impression of the epidermal cells. Abaxial epidermal structure is differentiated between intercostal and costal fields (Pl. 104, fig. 3). Intercostal cells are irregularly polygonal with gently curved walls, 40–60 μm in size (Pl. 104, fig. 3). Costal cells are more subrectangular and elongate, up to 140 μm long and 15–30 μm wide. A single papilla occurs in the centre of most abaxial cells, generally seen as a darkened spot on the cuticle, *c.* 10 μm in diameter (Pl. 104, fig. 5). In slightly undermacerated specimens, the papillae can be seen to conoidal with a broadly rounded apex, *c.* 10 μm high (Pl. 105, fig. 2). Larger trichome bases, 30–40 μm in diameter, also occur on both the costal and intercostal fields. Trichomes are multicellular files, each cell *c.* 50 μm long (Pl. 104, fig. 4). The most complete trichome fragments found are *c.* 140 μm long and 30 μm wide. Brachyparacytic stomata are distributed throughout intercostal fields, with polar axes approximately parallel to veins (text-fig. 16A). Sunken guard cells are 20–25 μm long and 3–4 μm wide (Pl. 105, figs. 3 and 4; text-fig. 16B–D). Subsidiary cells are slightly raised above the surrounding cells (Pl. 105, figs. 3 and 4). The number of subsidiary cells may vary from two to four. Stomatal Index varies from 9 to 11.

EXPLANATION OF PLATE 103

Figs. 1–4. *Neuropteris flexuosa* Sternberg. Cuticles photographed using Nomarski Contrast microscopy (except Fig. 1 using unpolarized light). 1, CCB/981GF-354/8; abaxial cuticle, Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), × 50. 2, CCB/977GF-268/3; close-up of abaxial cuticle showing stomata, Prince Mine, Point Aconi, Sydney Coalfield, 5–25 cm above Hub Seam, Morien Group (upper Westphalian D), × 125. 3, CCB/981GF-353/6; close-up of costal field showing papillae, Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), × 250. 4, CCB/981GF-353/6; close-up of sunken stomata with papillate guard cells, Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), × 250.

PLATE 103

CLEAL and ZODROW, *Neuropteris*
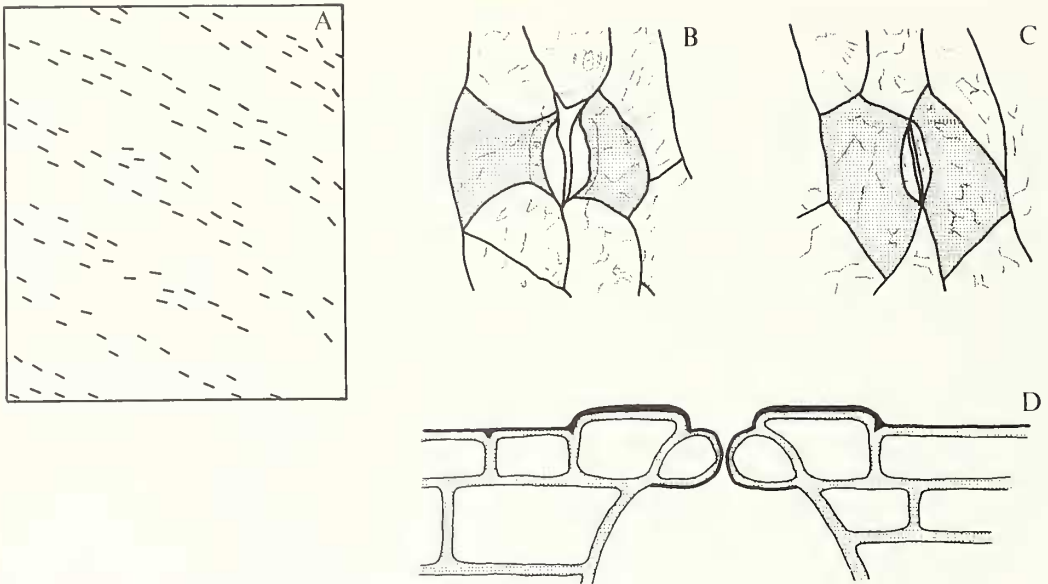
TEXT-FIG. 16. *Neuropteris macrophylla* Brongniart. Brogan's Pit near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D) 16A, CCB/982GF-229/4; general view of abaxial cuticle showing distribution and orientation of stomata, each stomatal polar axis being represented by a black line, × 35. 16B, CCB/982GF-229/13; close-up of stomatal apparatus, as viewed from outer surface of cuticle, with subsidiary cells stippled, × 500. 16C, CCB/982GF-229/7, close-up of stomatal apparatus, as viewed from outer surface of cuticle, with subsidiary cells stippled, × 500. 16D, reconstruction of stomatal apparatus prior to fossilization, thick black lines representing cutinized surfaces.

Rachial cuticles are relatively brittle, showing subrectangular to subrhomboidal epidermal cells in longitudinal rows (Pl. 104, fig. 2). The cells are 40–60 μm long and 30–40 μm wide, and often have a weakly developed papilla. Trichome bases are present near where pinnules are attached, and are 30–40 μm in diameter.

Remarks. This species occurs abundantly in the Westphalian D of eastern North America and the British Isles, but appears absent from the rest of Europe, including Saarland. There has been some debate as to its correct name. Kidston (1887) pointed out that *N. clarksonii* Lesquereux was probably a synonym of *N. macrophylla* Brongniart, and several authors have argued that Brongniart's illustrations are inaccurate and misleading (e.g. Bell 1938). At that early date, however, a species of fossil plant may be considered validly published with no illustration at all (ICBN Article 38), and is certainly not invalidated by an inaccurate illustration. The practical difficulties which might have arisen because of the poor illustration have been eliminated by Crookall (1959, pl. 42, figs. 1 and 1a) who published a photograph of the holotype.

EXPLANATION OF PLATE 104

Figs. 1–5. *Neuropteris macrophylla* Brongniart. Cuticles photographed using Nomarski Contrast microscopy (except Figs. 1 and 3, using unpolarized light), all specimens from Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), except Fig. 1, from Point Aconi, Sydney Coalfield, Point Aconi Seam, Morien Group (lower Cantabrian). 1, CCB/984GF-267/1; general view of adaxial cuticle, × 125. 2, CCB/982GF-229/6; cuticle from rachis, × 250. 3, CCB/982GF-229/1; abaxial cuticle, × 125. 4, CCB/982GF-229/4; broken trichomes from abaxial cuticle, × 250. 5, CCB/982GF-229/4, more weakly developed papillae, × 250.
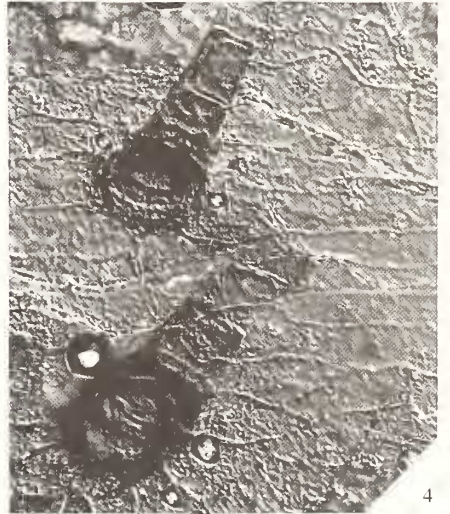
PLATE 104

CLEAL and ZODROW, *Neuropteris*
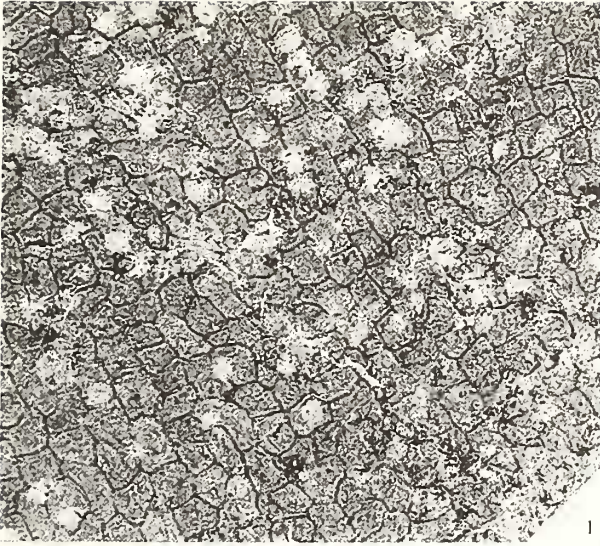
In *N. macrophylla* Brongniart, the lateral and terminal pinnules have most of the characteristic features of *Neuropteris*. However, the architecture of the frond appears somewhat different. The largest frond fragments to be illustrated in the literature (e.g. Crookall 1959, pl. 40, fig. 1; pl. 42, fig. 3) suggest that the frond consisted of bipinnate branches, presumably produced by a basal dichotomy, with intercalated pinnules on the primary racheis. This contrasts with the tripinnate structure with intercalated pinnae on the primary rachides of most other neuropterid fronds. However, the taxonomic significance of this difference is presently uncertain.

This species has a different epidermal structure from the neuropterid species already discussed in this paper. It differs in the relative uniformity of the adaxial cells, except along the midvein, and the presence of prominent stomatal subsidiary cells. The closest comparison is with *N. scheuchzeri* Hoffmann, *Neuropteris britannica* (Gutbier) and *N. subauriculata* Sterzel, which also have a more uniform adaxial cell structure, and stomata with subsidiary cells (Barthel 1961*b*, 1962; this study). The *N. britannica* (Gutbier) and *N. subauriculata* Sterzel stomata appear to be cyclocytic, but some seem to show a preferential thickening of the lateral subsidiaries giving them a brachyparacytic appearance (Barthel 1962, pl. 22, fig. 2; pl. 24, fig. 7). There is also an interesting similarity in frond architecture between these species. As with *N. macrophylla* Brongniart, *N. scheuchzeri* Hoffmann has bipinnate branches produced by the basal dichotomy and intercalated pinnules on the primary racheis (see discussion on next taxon). Daber (1955), described *N. britannica* (Gutbier) as also having a bipinnate structure. The evidence on which this is based is unclear, unless it is the specimen shown by Daber (1957, pl. 5, fig. 1), which is purported to be a dichotomous frond fragment with bipinnate branches. Little is known of the frond architecture of *N. subauriculata* Sterzel, but it had large pinnules (Daber 1955, pl. 19, fig. 2; pl. 25, fig. 4) comparable to those of *N. macrophylla* Brongniart and *N. scheuchzeri* Hoffmann.

Neuropteris scheuchzeri Hoffmann *in* Keferstein 1826

Plate 106; text-figs. 17 and 18

1826   *Neuropteris Scheuchzeri* Hoffmann *in* Keferstein, p. 157, pl. 1*b*, figs. 1–4.
1832   *Odontopteris obtusa* Brongniart; Lindley and Hutton (*non* Brongniart), pl. 40.
1833   *Odontopteris Lindleyana* Sternberg, p. 78
1847   *Odontopteris subcuneata* Bunbury, p. 427, pl. 23, figs. 1A, 1B.
1915   *Neuropteris Scheuchzeri* Hoffmann; Gothan, p. 379, pl. 32, figs. 5–8 (cuticles).
1930   *Neuropteris Scheuchzeri* Hoffmann; Bertrand, p. 24, pls. 9–12.
1938   *Neuropteris Scheuchzeri* Hoffmann; Bell, p. 57, pl. 50, figs. 3 and 4; pl. 51, figs. 1–5; pl. 52, figs. 1 and 2.
1938   *Odontopteris subcuneata* Bunbury; Bell, pp. 58, 62, pl. 57, figs. 1–8; pl. 58, figs. 1–3.
1959   *Neuropteris Scheuchzeri* Hoffmann; Crookall, p. 178, pl. 41, figs. 1 and 2; pl. 42, figs. 4–7; pl. 57, figs. 1, 2, 5.
1961*b* *Neuropteris scheuchzeri* Hoffmann; Barthel, p. 829, pl. 2; pl. 3, figs. 1–5 (cuticles).
1967   *Neuropteris scheuchzeri* Hoffmann; Laveine, p. 237, pls. 68 and 69.
1980*a* *Neuropteris scheuchzeri* Hoffmann; Zodrow and McCandlish, p. 47, pl. 37, figs. 2 and 3; pls. 38–42; pl. 43, fig. 1.
1982   *Neuropteris scheuchzeri* Hoffmann; Laveine and Brousmiche, p. 244, pl. 1, figs. 2 and 3.
1983   *Neuropteris scheuchzeri* Hoffmann; Beeler, p. 2361, figs. 28–37.
1985   *Neuropteris scheuchzeri* Hoffmann; Schabilion and Reihman, p. 3, figs. 1–29.

PLATE 105
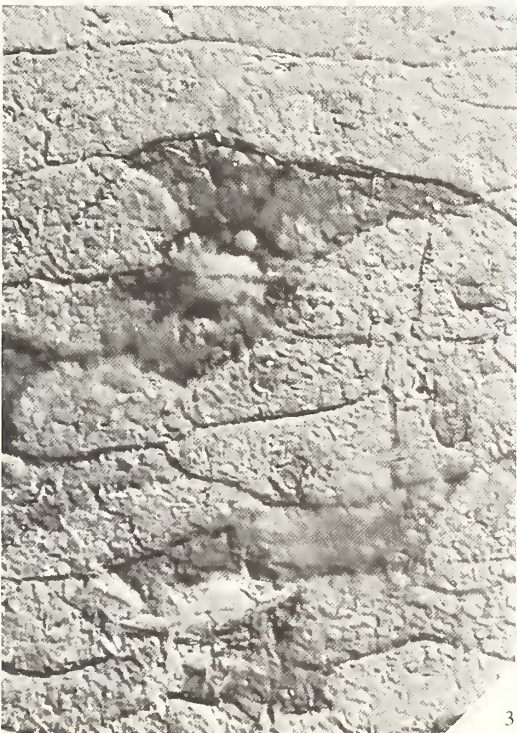
CLEAL and ZODROW, *Neuropteris*

TEXT-FIG. 17. *Neuropteris scheuchzeri* Hoffmann. 17A, 980GF-588; ultimate pinna terminal, Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), × 1. 17B, 985GF-245; isolated lateral pinnule, Point Aconi, Sydney Coalfield, Point Aconi Seam, Morien Group (lower Cantabrian), × 1.
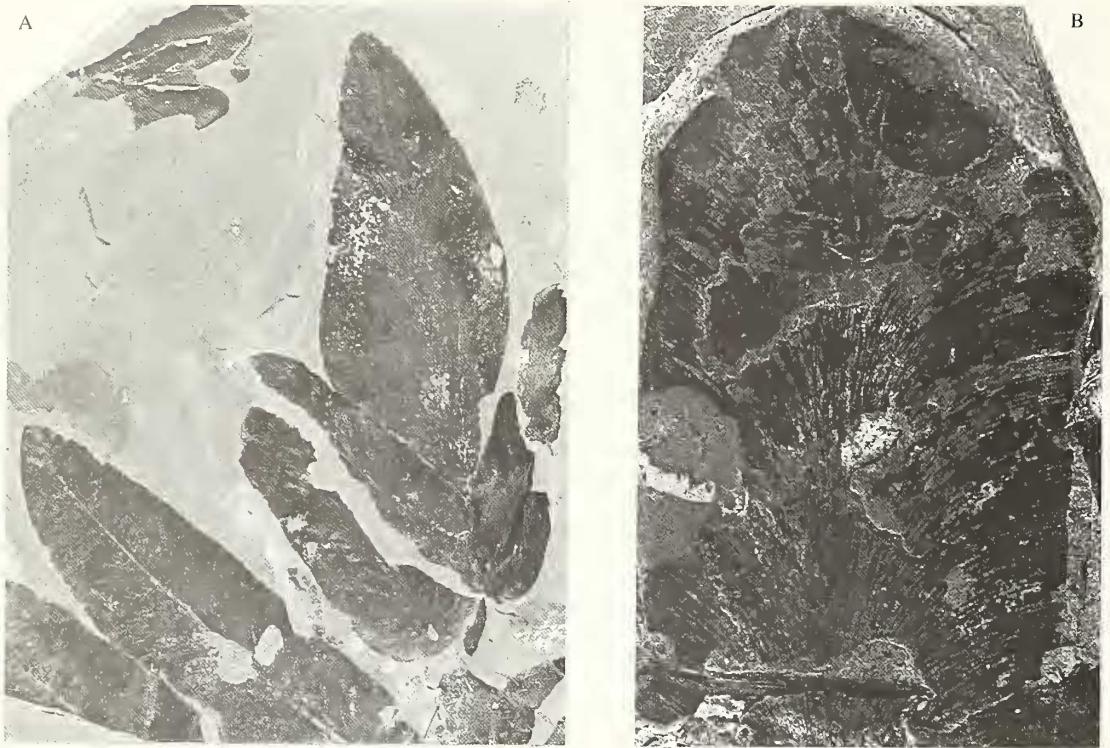
Gross morphology. Pinnate foliage bears large, lanceolate pinnules < 90 mm long and 25 mm wide, with an acuminate or slightly rounded apex (text-fig. 17). Pinnule bases are normally cordate, or with an unequally developed pair of rounded lobes (or 'pinnules') attached near base. Pinnules are usually entire-margined, but sometimes become laciniate (the '*Odontopteris lindleyana*' form). A prominent midvein extends for most of pinnule length. Dense lateral veins are attached at a low angle to the midvein, arch broadly, and meet the pinnule margin at 70–80°. Lateral veins fork 3–5 times. Pinnule surface is often covered by numerous adpressed hairs, 1·0–1·5 mm long. Over most of the pinnule, the hairs appear orientated towards the pinnule apex. Only near the pinnule base do the hairs seem orientated towards the pinnule lateral margins. Apical pinnules are large and lanceolate (text-fig. 17A).

EXPLANATION OF PLATE 106

Figs. 1–5. *Neuropteris scheuchzeri* Hoffmann. Cuticles photographed using Nomarski Contrast microscopy, all specimens from Brogan's Pit, near Point Aconi, Sydney Coalfield, *c.* 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D), except Fig. 1, from Point Aconi, Sydney Coalfield, Point Aconi Seam, Morien Group (lower Cantabrian). 1, CCB/985GF-245/8; cuticle from adaxial surface of pinnule, × 125. 2, CCB/985GF-245/12; cuticle from abaxial surface of pinnule, × 125. 3, CCB/980GF-588/7; slightly under-macerated cuticle from abaxial surface of pinnule, × 125. 4, CCB/985GF-245/14; close up of stomata on abaxial surface of pinnule, × 500. 5, CCB/985GF-245/12; close up of stomata on abaxial surface of cuticle, × 500.

PLATE 106

CLEAL and ZODROW, *Neuropteris*
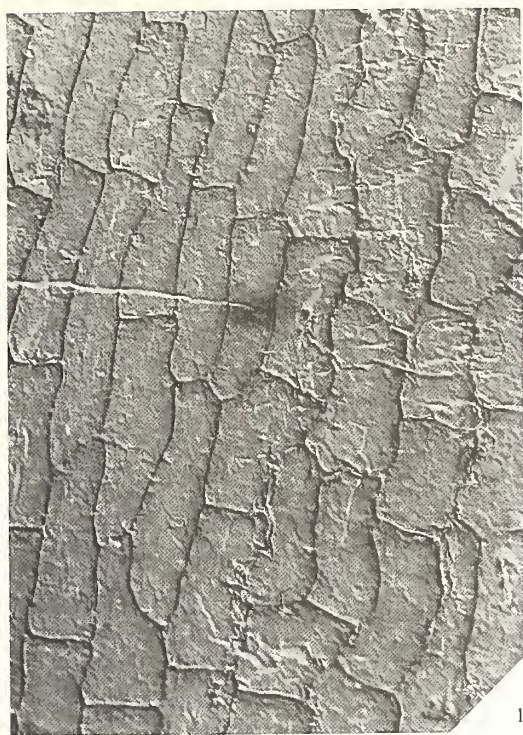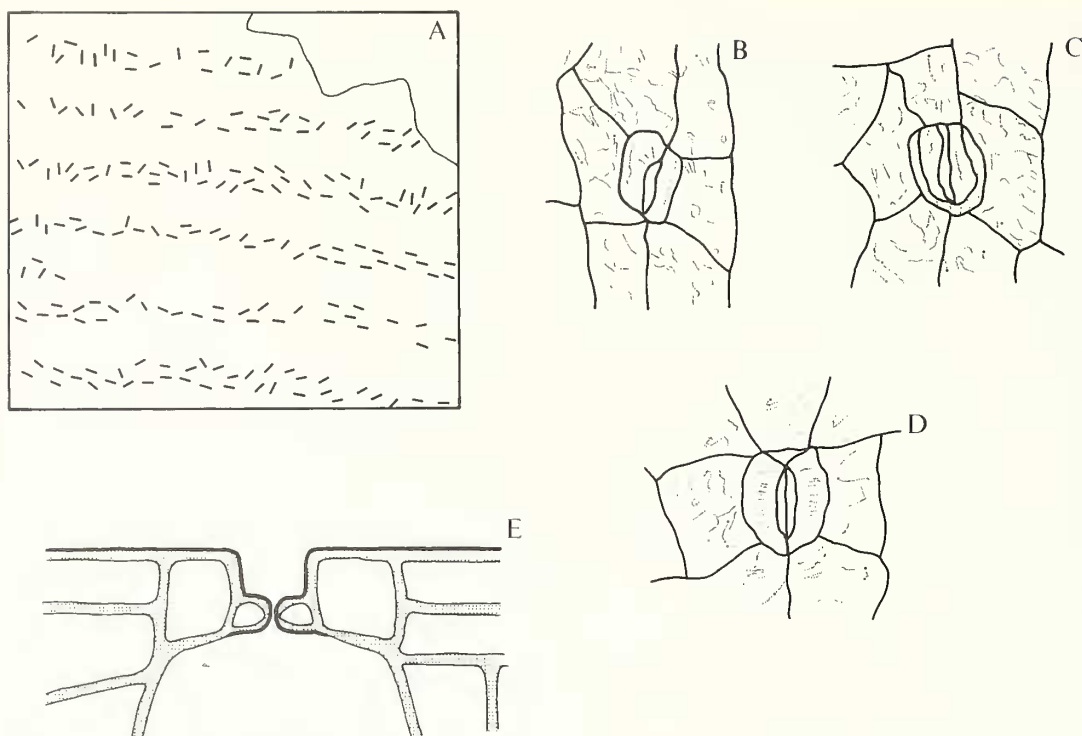
TEXT-FIG. 18. *Neuropteris scheuchzeri* Hoffmann. 18A, C from Point Aconi, Sydney Coalfield, Point Aconi Seam, Morien Group (lower Cantabrian), 18B, D from Brogan's Pit, near Point Aconi, Sydney Coalfield, c. 8 m above Lloyd Cove Seam, Morien Group, (upper Westphalian D). 18A, CCB/980GF-588/7; general view of abaxial cuticle showing distribution and orientation of stomata, each stomatal polar axis being represented by a black line, × 35. 18B, CCB/985GF-245/14; close-up of stomatal apparatus, as viewed from the outer surface of cuticle, × 500. 18C, CCB/980GF-588/7; close-up of stomatal apparatus, as viewed from outer surface of cuticle, × 500. 18D, CCB/985GF-245/8, close-up of stomatal apparatus, as viewed from inner surface of cuticle, × 500. 18E, reconstruction of stomatal apparatus prior to fossilization, thick black lines representing cutinized surfaces.

Epidermal structure. Adaxial epidermal structure is weakly differentiated between intercostal and costal fields (Pl. 106, fig. 1). Cells are irregularly polygonal, up to 220 µm and 60 µm wide, and sometimes with broadly sinuous margins. Trichomes are restricted to area near midvein. Trichome bases vary in diameter from 20–60 µm. Only short stumps of these trichomes, up to 150 µm long, are still attached to the cuticle and show no cellular detail.

Abaxial epidermal structure is differentiated between intercostal and costal fields (Pl. 106, fig. 2). Intercostal cell are irregularly polygonal, 40–60 µm in size, have gently curved walls. Costal cells are more subrectangular and elongate, up to 200 µm long and 10–30 µm wide. The abaxial cuticle is densely covered with trichome bases, which vary considerably in diameter from 10 to 45 µm (Pl. 106, figs. 2 and 3). These bases occur on both intercostal and costal fields, but the larger ones tend to be concentrated on the latter. The trichomes themselves were not seen. Stomata are densely distributed throughout intercostal fields, with polar axes showing a random orientation (text-fig. 18A). Guard cells are 25 µm long and 4 µm wide, and lie in a deep stomatal pit (text-fig. 18B–E). Subsidiary cells are brachyparacytic (Pl. 106, figs. 4 and 5). Stomatal Index varies from 9 to 14.

Remarks. The taxonomy of this species is fairly straightforward, and has been adequately discussed by Crookall (1959) and Laveine (1967). A recently reported specimen indicates that the frond consisted of two bipinnate branches produced by a dichotomy near the base (Laveine and Brousmiche 1982, pl. 1, fig. 3), whilst the large specimen figured by Bertrand (1930, pl. 9) shows that

there were intercalated pinnules on the primary racheis. This structure differs from that seen in most neuropterid species, in which the primary branches produced by the basal dichotomy were tripinnate, and the intercalated elements on the primary branches were pinnate. Consequently, Laveine (1967) has interpreted *N. scheuchzeri* Hoffmann as being a retarded form of the typical neuropterid frond.

Another unusual aspect of the *N. scheuchzeri* Hoffmann frond is the presence of laciniate pinnules, which, in the early literature, were referred to as *Odontopteris lindleyana* Sternberg and *O. subcuneata* Bunbury. Bode (1958) compared them with the aphlebia (or stipules – Hill and Camus 1986, p. 238) of many marattialean ferns, but there is no evidence that they fulfilled a similar functional role. Laveine (1967) correctly argued that they were probably attached near the base of the frond. In analogy, similar fimbriate pinnules have been reported from what is probably near the base of the *Neuropteris obliqua* (Brongniart) frond (Stockmans 1933, pl. 12, fig. 2; Laveine 1967, pl. 54, fig. 1).

As remarked by Barthel (1961 b), it is difficult to prepare good cuticles from this species, particularly from the abaxial surface. The cuticle is not particularly thin, but can be very difficult to clear (e.g. Pl. 106, fig. 3). However, a few of the cuticles prepared during this study have shown the stomatal structure, in particular the presence of a pair of lateral subsidiary cells (Pl. 106, figs. 4 and 5). Barthel (1961 b) does not regard these as true subsidiary cells and, indeed, they are not thickened or raised above the pinnule surface as in *N. macrophylla* Brongniart. However, a pair of cells does seem to occur consistently in a lateral position and so we interpret them as subsidiaries.

The epidermal structures described for this species by Barthel (1961 b), based on specimens from the Westphalian C of Saarland, appear identical to those seen in the Canadian specimens. He stated that there is little differentiation between the costal and intercostal cells on the adaxial surface. We acknowledge that the differentiation is not particularly strong, but it is there (Pl. 106, fig. 1) and can also be recognized in the Saarland specimens (Barthel 1961 b, pl. 2, fig. 7; pl. 3, fig. 2). We can find no features which clearly differentiate the Saarland and Canadian specimens.

This apparent identity in epidermal structure is of interest since there are minor gross-morphological differences between specimens from the two areas. The most obvious difference is the abundance of the laciniate (*Odontopteris lindleyana*-type) pinnules in the Canadian assemblages, and its virtual absence in the Saarland specimens. The significance of this difference has never been properly determined, but is not reflected in the epidermal evidence.

There also seems to be a close similarity with the epidermal structures described from permineralized specimens (Beeler 1983; Schabilion and Reihman 1985). In particular, a brachyparacytic stomatal configuration seems to be indicated by Beeler (1983, fig. 37). No evidence has been found, either by Barthel (1961 b) or us, of the overhanging papillae around the stomata reported by Schabilion and Reihman (1985). Their presence is mainly supported by fig. 27 in Schabilion and Reihman's paper, which shows a deep stomatal pit and what appear to be overhanging protrusions from the surrounding cells. However, they do not appear to be particularly noticeable around the stomata shown in their fig. 29 and we wonder if the structures visible in their other specimen may be a function of preservation.

Based on epidermal evidence, *N. scheuchzeri* Hoffmann appears to be most closely related to *N. macrophylla* Brongniart, *N. subauriculata* Sterzel and *N. britannica* (Gutbier). The weak differentiation of the adaxial costal and intercostal cells, the brachyparacytic arrangement of the subsidiary cells and the low (relative to the other neuropterid species) Stomatal Index support this. As already discussed, there are also similarities in frond architecture between these four species.

DISCUSSION

Taxonomy

Cuticles from 17 imparipinnate neuropterids have now been described in the literature. Of these, *N. planchardii* Zeiller and *N. cordata* Brongniart clearly stand out from the rest, being amphistomatic

TABLE 1. Principal cuticular features of Groups I and II *Neuropteris* species. Based on this study, and data from Barthel (1962), Daber (1963), Saltzwedel (1968), Oestry-Stidd (1979) and Cleal (1985).

	Group I					Group II		
	N. loshii	N. tenuifolia	N. rarinervis	N. simonii	N. sarana	N. aconiensis	N. flexuosa	N. schaeferi
Form of rachial cells	Elongate	Elongate	Elongate	Isodiametric	Isodiametric	?	Isodiametric	?
Maximum dimensions of rachial cells (μm)	300 × 30	80 × 30	100 × 30	100 × 100	70 × 70	?	50 × 50	?
Diameter of trichome bases on rachis (μm)	40	30-45	None present	20-40	25	?	60	?
Distribution of cells in adaxial epidermis	Uniform	Uniform	Uniform	Different in costal fields	Different in costal fields	Uniform	Different in costal fields	Different in costal fields
Adaxial cell walls sinuous?	No	No	Yes	Yes	Yes	No	No	Yes
Maximum size of adaxial intercostal cells (μm)	200 × 25	500 × 80	300 × 35	80 × 45	120 × 60	60 × 60	200 × 50	?
Maximum size of adaxial costal cells (μm)	200 × 25	500 × 80	300 × 35	200 × 25	200 × 30	60 × 60	200 × 25	?
Adaxial papillae	None	None	None	None	None	None	None	None
Adaxial multicellular files	None	None	None	None	None	None	None	None
Diameter of adaxial trichome bases (μm)	-	-	-	-	-	-	-	-
Abaxial cells visible?	No	No	No	Yes	Yes	Yes	Yes	Yes
Maximum size of abaxial intercostal cells (μm)	-	-	-	120 × 120	75 × 75	60 × 60	100 × 100	?
Maximum size of abaxial costal cells (μm)	-	-	-	250 × 25	150 × 30	200 × 40	150 × 25	?
Abaxial papillae	None	None	None	None	None	None	Present	None
Abaxial multicellular files	None	Rare, only near midvein	Rare	Present	Present	None	Present	Present
Diameter of abaxial trichome bases (μm)	-	10-20	20-30	20-30	50	-	50	?
Structure of stomata	? anomocytic	? anomocytic	anomocytic	anomocytic/ brachyparacytic	anomocytic/ brachyparacytic	anomocytic	anomocytic	anomocytic
Orientation of stomata	Parallel to veins	Parallel to veins	Parallel to veins	Parallel to veins	Parallel to veins	Parallel to veins	Parallel to veins	Parallel to veins
Stomatal density (per mm²)	200	300	140	90	28	50	120	?
Stomatal Index	-	-	-	30-35	25-30	17-19	15-18	?
Guard cell length (μm)	15-25	20-25	20-30	15-30	18-30	10-20	20-25	?

TABLE 2. Principal cuticular features of Groups III and IV *Neuropteris* species. Based on this study, and data from Barthel (1961*b*, 1962, 1976)

	Group III						Group IV
	N. scheuchzeri	N. macrophylla	N. britannica	N. subauriculata	N. sp. a	N. sp. b	N. neuropteroides
Form of rachial cells	?	Slightly elongate	?	?	?	?	Isodiametric
Maximum dimensions of rachial cells (µm)	?	60 × 40	?	?	?	?	?
Diameter of trichome bases on rachis (µm)	?	30–40	?	?	?	?	None present
Distribution of cells in adaxial epidermis	Uniform	Different along midvein	Different along midvein	Uniform	Uniform	Different in costal fields	Uniform
Adaxial cell walls sinuous?	No	No	No	No	No	No	No
Maximum size of adaxial intercostal cells (µm)	220 × 60	60 × 60	70 × 40	100 × 20	45 × 20	80 × 60	100 × 20
Maximum size of adaxial costal cells (µm)	220 × 60	60 × 60	70 × 40	100 × 20	45 × 20	60 × 15	100 × 20
Adaxial papillae	None	None	None	Present	None	None	Near midvein
Adaxial multicellular files	Only near midvein	None	Only near midvein	Rare	None	None	None
Diameter of adaxial trichome bases (µm)	20–60	–	25–35	20–25	–	–	–
Abaxial cells visible?	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Maximum size of abaxial intercostal cells (µm)	60 × 60	60 × 60	50 × 50	65 × 35	45 × 18	40 × 40	25 × 25
Maximum size of abaxial costal cells (µm)	200 × 30	140 × 30	140 × 15	80 × 30	200 × 18	80 × 12	25 × 25
Abaxial papillae	None	Present	None	Present	None	Present	Present
Abaxial multicellular files	Present	Present	Rare	Present	None	None	None
Diameter of abaxial trichome bases (µm)	20–60	30–40	15–20	20–25	–	–	–
Structure of stomata	brachyparacytic	brachyparacytic	brachyparacytic/ cyclocytic	brachyparacytic/ cyclocytic	brachyparacytic/ cyclocytic	brachyparacytic/ cyclocytic	amphicyclocytic
Orientation of stomata	Random	Parallel to veins	Parallel to veins	Parallel to veins	Parallel to veins	Parallel to veins	Parallel to veins
Stomatal density (per mm²)	90	65	130	91	180	180	?
Stomatal Index	9–14	9–11	?	?	?	?	?
Guard cell length (µm)	25	20–25	18–25	20–30	25–35	20–25	17–22

(Reichel and Barthel 1964; Barthel 1976). No other form-species of trigonocarpalean frond is known to be amphistomatic, and it is a character more usually associated with another order of late Palaeozoic pteridosperms, the Peltaspermales (Townrow 1960; Barthel 1962; Barthel and Haubold 1980; Kerp 1986).

The principal epidermal characters of the remaining 15 species and varieties are summarized in Tables 1 and 2. There are many points of similarity between them: they are all hypostomatic; the stomata have a relatively simple arrangement of subsidiary cells, if any at all; and the trichomes are either simple papillae or multicellular files without glandular tips. It is possible to subdivide the group using other epidermal features (the so-called *N. heterophylla* Brongniart of Wills (1914) is omitted from this analysis because of doubt as to its true identity).

Group I: Adaxial epidermal cells weakly differentiated between costal and intercostal fields. Virtually no cell structure visible on abaxial cuticle, other than guard cells. Stomata probably anomocytic. Trichomes absent or very rare.

    N. loshii Brongniart (Daber 1963)
    N. tenuifolia Sternberg (Barthel 1962)
    N. rarinervis Bunbury (This study)

This appears to be the group of neuropterids whose frond had a basal dichotomy producing tripinnate branches, with intercalated pinnae on the antepenultimate racheis and orbicular cyclopterids near the frond base (e.g. von Roehl 1868, pl. 17, Laveine 1967, pl. 45, fig. 3).

Group II: Adaxial epidermal cells strongly differentiated between costal and intercostal fields. Cell structure clearly visible on abaxial cuticle, and strongly differentiated between costal and intercostal fields. Stomata anomocytic, or brachyparacytic with non-thickened subsidiary cells. Numerous trichomes on abaxial surface only, either papillae and/or multicellular files.

> *N. ovata* var. *simonii* (Bertrand) (This study)
> *N. ovata* var. *sarana* (Bertrand) (This study)
> *N. ovata* var. *aconiensis* var. nov. (This study)
> *N. flexuosa* Sternberg (This study)
> *N. schaeferi* Doubinger and Germer (Saltzwedel 1968)

This appears to correspond to the form-genus *Mixoneura* Bertrand, 1930 (*non* Weiss 1870). The frond architecture is similar to that of the Group I species except that, instead of orbicular cyclopterids, there are pinnae bearing fimbriate pinnules at the base of the frond (Zodrow and Cleal 1988).

Group III: Adaxial epidermal cells weakly differentiated between costal and intercostal fields (except along midvein). Cell structure clearly visible on abaxial cuticle, and strongly differentiated between costal and intercostal fields. Stomata brachyparacytic, rarely cyclocytic, with thickened or non-thickened subsidiary cells. On adaxial cuticle, multicellular file trichomes absent or restricted to midvein. Numerous trichomes on abaxial surface, both multicellular files and sometimes papillae.

> *N. scheuchzeri* Hoffmann (This study)
> *N. macrophylla* Brongniart (This study)
> *N. britannica* (Gutbier) (Barthel 1962)
> *N. subauriculata* Sterzel (Barthel 1962)
> *N.* sp. α (Barthel 1962)
> *N.* sp. β (Barthel 1962)

This group consists, at least in part, of species with retarded fronds (*sensu* Laveine 1967). The first two species have essentially bipinnate branches produced by a basal dichotomy, and rather large lateral pinnules (Crookall 1959; Laveine 1967). *N. britannica* (Gutbier) is also reported to have a bipinnately divided frond (Daber 1955, 1957). *N. subauriculata* Sterzel has large pinnules within its frond, but full details of the frond architecture are unknown (Daber 1955). Details of the frond of Barthel's *N.* sp. α and *N.* sp. β are unknown.

Group IV: Adaxial epidermal cells weakly differentiated between costal and intercostal fields. Cell structure clearly visible on abaxial cuticle, and weakly differentiated between costal and intercostal fields. Stomata amphicyclocytic. Multicellular file trichomes absent, but strongly developed papillae occur on abaxial surface.

> *N. neuropteroides* (Göppert) (Barthel 1962)

This species is strikingly similar to *N. ovata* Hoffmann, and Zalessky (1909) argued that the two are conspecific. Corsin (*in* Pruvost and Corsin 1949) instead suggested that *N. neuropteroides* (Göppert) is the Permian descendant of *N. ovata* Hoffmann. Support for Corsin's view was given by Wagner and Lemos de Sousa (1983), who reported an apparently intermediate species (*N. pseudovata* Gothan and Sze) from the lower Stephanian C of Portugal. Known details of the *N. neuropteroides* (Göppert) frond architecture (Barthel 1976; Šetlík 1980) would seem to support this hypothesis. However, it is difficult to reconcile it with the marked difference in epidermal structure, which suggest that *N. neuropteroides* (Göppert) belongs to a quite distinct group of plants.

It is clear from the above that, by combining data on frond architecture and epidermal structure, we are starting to recognize more natural groups of species within the presently accepted circumscription of *Neuropteris*. More data are needed before any formal proposals are made. In particular, the epidermal structure of the type-species (*N. heterophylla* Brongniart emend. Laveine)

requires determination, as well as that of some of the other commonly occurring neuropterids (e.g. *N. obliqua* (Brongniart)). More information is also needed about the frond architecture of some of the species, particularly those in our Group III. For the time being, therefore, it is probably wisest to retain the traditional concept of the form-genus as outlined earlier in this paper.

Amongst other form-genera of medullosan foliage, the most comparable cuticles have been reported from *Odontopteris* (Barthel 1961 *b*, 1962). They are hypostomatic, with anomocytic stomata restricted to the intercostal fields, and sparsely distributed multicellular files restricted to the abaxial cuticle. The main difference appears to be the more random orientation of the stomatal polar axes in *Odontopteris* (except compared with *N. scheuchzeri* Hoffmann – text-fig. 18A). This supports the view of Wagner (*in* Harland *et al.* 1967) that the two form-genera belong to the same family, the Cyclopteridaceae, rather than different families as argued by Corsin (1960) mainly on the basis of pinnule morphology.

Several points of similarity exist with alethopterid cuticles (Zeiller 1890; Wills 1914; Barthel 1962, 1963), in particular the restriction of the stomata to the intercostal fields of the abaxial cuticle. The stomata themselves are either anomocytic or cyclocytic, with no evidence of the brachyparacytic stomata seen in the Group III neuropterids. The cuticles of most *Alethopteris* species seem to be much thicker, often densely ornamented by robust papillae, which contrasts with the more delicate cuticle bearing (sometimes) smaller papillae in all but the Group IV neuropterids. The multicellular files on the abaxial surface of *Alethopteris* pinnules have some similarity to those of *Neuropteris*, except that the component cells are usually shorter relative to their width. However, they seem to be much denser in *Alethopteris*, particularly near the midvein (cf. Barthel 1962, pl. 33, figs 1 and 4) and in at least one species have been shown to have glandular tips (Barthel 1962, pl. 34, fig. 4).

The epidermal structure of *Callipteridium* foliage is poorly known. The cuticles of only one species probaby belonging to the form-genus have been described (Barthel 1962), i.e. '*Alethopteris*' *subdavreuxii* Sterzel. This species has intercalated pinnae on the antepenultimate racheis (Daber 1955, pl. 22, fig. 1) and is almost certainly a *Callipteridium*, probably allied to *C. armasii* (Zeiller). Its cuticle has many features in common with *Neuropteris*, in particular the stomata being restricted to the abaxial intercostal fields. However, the '*Alethopteris*' *subdavreuxii* Sterzel stomata seem to be rather more regularly tetracytic than in *Neuropteris*. There is also a complete absence of epidermal trichomes, which is only really typical of the Group I neuropterids.

Laveine *et al.* (1977) regard *Palaeoweichselia defrancei* (Brongniart) as being closely related to *Callipteridium*, and the cuticle of this species has been described by Barthel (1961 *b*). *P. defrancei* (Brongniart) is hypostomatic, with anomocytic stomata restricted to the intercostal fields, but the stomata seem much denser and have a more random orientation than in *Neuropteris*. The epidermal trichomes of *P. defrancei* (Brongniart) appear very similar to those of *Neuropteris*.

The Rachivestitaceae medullosans (*sensu* Bertrand 1930, Corsin 1960 – i.e. *Paripteris* and *Linopteris*) also show many of the epidermal characteristics of *Neuropteris*, including the presence of anomocytic or cyclocytic stomata restricted to the abaxial intercostal fields. However, the adaxial surface of many of the species (e.g. *Paripteris gigantea* (Sternberg), *Linopteris neuropteroides* (Geinitz), *L. brongniartii* (Gutbier)) are densely covered by robust trichomes (Barthel 1961 *b*, 1962), which are either absent or rare in *Neuropteris*. This is not a clear-cut means of distinguishing them since adaxial trichomes appear absent in some linopterids, such as *L. weigelii* (Sterzel) (Barthel 1962).

Cyclopterid pinnules

No attempt has been made here to study cuticles from the cyclopterid pinnules, which are widely believed to occur at the base of the neuropterid fronds. Although we had available a number of cyclopterids found in association with pinnate neuropterid foliage, none was found directly attached to fronds to confirm their identity. There are, nevertheless, some records in the literature which allow relevant comments to be made on these structures. Two basic types of cyclopterids can be recognized based on their epidermal structure.

Type A. Amphistomatic cyclopterids, usually identified as Cyclopteris orbicularis Brongniart *and* C. trichomanoides *Brongniart.* Florin (1925) pointed out that this type of cyclopterid is associated with pinnate foliage belonging to *Neuropteris tenuifolia* Sternberg, *N. heterophylla auct. non* Brongniart (syn. *N. loshii* Brongniart) and *N. rarinervis* Bunbury, corresponding to the Group I neuropterids as defined in this paper. They are attached singly and directly to the primary rachis near the base of the frond (von Roehl 1868, pl. 17; Carpentier 1930, pl. 8; Laveine 1967, pl. 45, fig. 3). They also appear to have had quite a different epidermal structure from the pinnate foliage. For instance, the cyclopterids associated with *N. tenuifolia* Sternberg have brachyparacytic/cyclocytic stomata (Florin 1925, pl. 8, figs. 1–8), whereas the pinnate foliage probably has anomocytic stomata (Barthel 1962, pl. 17, figs. 3–8; Cleal 1985).

Type B. Hypostomatic cyclopterids, in which the epidermal structure is essentially similar to that of associated neuropterid pinnate foliage. The following correlations between cyclopterid and neuropterid pinnate foliage have been established by Barthel (1962), based on cuticular evidence.

Pinnate foliage	Cyclopterids
N. ovata var. *simonii* (Bertrand)	*Cyclopteris* sp. (*sensu* Florin 1926)
N. subauriculata Sterzel	*Cyclopteris felixii* Florin
N. sp. β (*sensu* Barthel 1962)	*Cyclopteris crassinervis* Göppert

These include representatives of Groups II and III neuropterids (as defined in this paper). In at least one case (*N. ovata*), the cyclopterids are attached to slender racheis at the base of the frond (Zodrow and Cleal 1988).

It is evident that the classification of pinnate neuropterid foliage proposed in this paper is at least partly supported by the evidence from the cyclopterids: Group I neuropterids have Type A cyclopterids, and Groups II and III neuropterids have Type B cyclopterids.

The Type A and Type B cyclopterids seem to be quite different in nature. Type B cyclopterids are evidently just large leaflets from near the base of the frond, differing little from the neuropterid pinnules except in size. Type A cyclopterids differ significantly from the neuropterid foliage, particularly in being amphistomatic and it is difficult to see them simply as modified pinnate lamina from the base of the frond. Potonié (1903) argued that they were stipules, for the protection of the young frond, but Florin (1926) pointed out that their epidermal structure does not support this view. It is also difficult to reconcile the stipule theory with the report of a 127 cm long rachis/petiole with cyclopterids attached (Seward 1888). That the Type A cyclopterids are densely stomate indicates that, at least in the fully developed frond, they fulfilled a photosynthetic role, but whether they had another role at other growth stages remains uncertain. They certainly developed in a quite different way from the pinnate foliage.

Biostratigraphy

N. ovata Hoffmann has a considerable biostratigraphical significance, being the main index to the base of the Westphalian D Stage (Cleal 1984*a*). How, then, does the recognition of at least three varieties of this species affect its robustness in this role? At least in the Saarland, Sydney and probably Nord-Pas-de-Calais coalfields, *N. ovata* var. *simonii* (Bertrand) is the stratigraphically lowest variety to occur. In northern Germany, *N. ovata* Hoffmann var. *ovata* is reported to occur at the base of the Westphalian D (Saltzwedel 1969) but, in the absence of epidermal evidence, it is impossible to say how these specimens relate to var. *simonii*. *N. ovata* var. *sarana* (Bertrand) and *N. ovata* var. *aconiensis* nov. var. occur in the upper Westphalian D and lower Cantabrian respectively (*N. ovata* var. *grandeuryi* Wagner, recognized on gross morphological features, is an exclusively Stephanian variety – Wagner 1963). There was evidently a gradual change in *N. ovata* with time, possibly as a result of genetic drift, with var. *simonii* (Bertrand) appearing in the early Westphalian D, but being replaced by var. *sarana* (Bertrand), var. *aconiensis* var. nov. and var. *grandeuryi* Wagner in the late Westphalian D and Stephanian. Since only the var. *simonii* probably occurs in the lower Westphalian D, the species may still be regarded as a robust means of recognizing the stage boundary.

We have stated previously (Zodrow and Cleal 1985) that the lowest occurrence of *N. flexuosa* Sternberg can also be used to recognize the base of the Westphalian D. The evidence presented in this paper clearly shows that it is quite distinct from *N. ovata* Hoffmann, and not just a form as suggested by Crookall (1959). The South Wales records nevertheless indicate that the first occurrences of both species occur at about the same level (Cleal 1978). The lowest occurrence of *N. flexuosa* Sternberg may therefore still be used as a guide to the stage boundary, although additional evidence from areas yielding both species will be needed to confirm its homotaxial reliability.

Palaeoecology

As pointed out by Harris (1956), cuticle characters can sometimes indicate the climatic conditions prevailing when the plant grew. Such evidence must always be treated with circumspection, since apparently xeromorphic characters may in fact be a response to restricted water absorption by the roots (e.g. the plant may have grown in high salinity soils, high light-levels or even nitrogen deficiency), rather than dry atmospheric conditions. Nevertheless, such characters may provide invaluable indices to the original habitat of the plant.

There is in fact little obvious evidence of defence against excessive water loss in these neuropterid cuticles. The majority have extremely thin cuticles and relatively abundant stomata. Fritsch and Salisbury (1953) pointed out that plants growing in a dry habitat sometimes develop unusually large epidermal cells, in which water can be conserved, but there is no evidence of this in *Neuropteris*. Furthermore, the neuropterid stomata are of a size normally found in plants growing in a humid atmosphere and moist soils (Wilkinson *in* Metcalfe and Chalk 1979). Barthel (1962) reported some neuropterid species to have guard cells at the bottom of cutinized pits, a feature often regarded as xeromorphic. This is a difficult feature to observe in light-microscope studies, and could not be clearly established by us. The only strongly papillate species is *N. neuropteroides* (Göppert), but Barthel (1962) did not note any marked thickening of its cuticle, except at the edge of the pinnule.

In present-day angiosperm floras, hypostomatic leaves are more commonly found in low altitude floras (Wilkinson *in* Metcalfe and Chalk 1979). This would confirm that the neuropterid species grew in low altitudes, rather than being the transported remains of high altitude plants. However, in the absence of evidence on stomatal distribution in high altitude Carboniferous floras (assuming that they existed) it is possible simply that the hypostomatic condition is the primitive state.

The presence of abundant epidermal trichomes on the stomatal-bearing surfaces is sometimes an attempt to reduce transpiration in wind. Few of the neuropterid cuticles showed densely distributed trichomes, although some are usually present (except the Group I species). The most notable exception is *N. scheuchzeri* Hoffmann, with its abundant multicellular files on the abaxial surface. It is interesting that *N. scheuchzeri* Hoffmann usually occurs in compression floras as isolated pinnules, examples of large pinnae (e.g. Bertrand 1930, pl. 9) being extremely rare. This may reflect that the plant grew in a somewhat higher (? and drier) habitat within the swamp-area, and that the frond-fragments had to undergo rather greater transportation than the other neuropterid species. Species growing in a more elevated habitat would of course be more exposed to the drying effects of the wind, and the denser trichomes may be a response to this (cf. also the report of apparently xeromorphic characters in *N. scheuchzeri* Hoffmann by Schabilion and Reihman 1985).

Schabilion and Reihman (1985) have argued that the xeromorphic characters in *N. scheuchzeri* Hoffmann fronds may be due to their having grown and developed in full sun-light. The apparently thicker limb of *N. scheuchzeri* Hoffmann pinnules is used to support this argument, but it may alternatively be a response to wind-induced mechanical stress (see previous paragraph). They also mention the relatively high vein density of *N. scheuchzeri* Hoffmann, but it is in fact little greater than that of many other neuropterid species, such as *N. ovata* Hoffmann. Further the stomatal density, which is lower in *N. scheuchzeri* Hoffmann in both absolute terms and the Stomatal Index, does not support Schabilion and Reihman's hypothesis. In our view, the evidence suggests that the anomalous characters of *N. scheuchzeri* Hoffmann are the result of mechanical (wind-induced) stress, rather than because they were sun leaves.

There is little evidence in these neuropterid cuticles of a defence strategy against insect attack,

such as the glandular trichomes reported in *Mariopteris* (Kidston 1925). This is of interest since evidence of insect damage is relatively rare in these fossil leaves (Taylor and Scott 1983), or is at least difficult to distinguish from taphonomic damage. Many Carboniferous insects were at least partly carnivorous (Bolton 1922; North 1931), but it is difficult to see why some pteridosperm foliage (e.g. *Mariopteris*) had to develop glandular trichomes if they were not at risk from insect attack. One can only speculate that the levée-top habitat of the neuropterid species somehow prevented access by the bulk of the insects or, perhaps more likely, they had developed some alternative strategy, such as a chemical defence.

APPENDIX

Summary of provenance for specimens described in this paper.
SYDNEY COALFIELD
N. rarinervis Bunbury
   1. 982GF-274 (19 slides) Brogan's Pit, near Point Aconi, Sydney Coalfield. Above Lloyd Cove Seam, Morien Group (upper Westphalian D).
   2. 982GF-275 (6 slides) Brogan's Pit, near Point Aconi, Sydney Coalfield. Above Lloyd Cove Seam, Morien Group (upper Westphalian D).

N. ovata Hoffmann var. *simonii* (Bertrand)
   1. 982GF-405 (10 slides) Point Aconi, Sydney Coalfield. About 1 m above the Point Aconi Seam, Morien Group (lower Cantabrian).
   2. 977GF-126 (3 slides) Private drift mine 1 km west of Steele's Road, Glace Bay, Sydney Coalfield. Emery Seam, Morien Group (middle Westphalian D – lowest reported occurrence in Sydney Coalfield – Zodrow and Cleal 1985).
   3. 979GF-230 (4 slides) Prince Mine, Sydney Mines, Sydney Coalfield. Morien Group, exact horizon unknown (? Westphalian D).

N. ovata Hoffmann var. *aconiensis* var. nov.
   1. 985GF-236 (14 slides) Point Aconi, Sydney Coalfield. Point Aconi Seam, Morien Group (lower Cantabrian).

N. flexuosa Sternberg
   1. 977GF-267 (7 slides) Prince Mine, Point Aconi, Sydney Coalfield. 5–25 cm above Hub Seam, Morien Group (upper Westphalian D).
   2. 977GF-268 (4 slides) Prince Mine, Point Aconi, Sydney Coalfield. 5–25 cm above Hub Seam, Morien Group (upper Westphalian D).
   3. 981GF-353 (8 slides) Brogan's Pit, near Point Aconi, Sydney Coalfield. 20–35 cm above unnamed seam, *c.* 8 metres above Lloyd Cove Seam, Morien Group (upper Westphalian D).

4. 981GF-354 (11 slides) Brogan's Pit, near Point Aconi, Sydney Coalfield. 20–35 cm above unnamed seam, *c.* 8 m above Lloyd Cove Seam, Morien Group (upper Westphalian D).

N. macrophylla Brongniart
1. 982GF-229 (17 slides) Brogan's Pit, near Point Aconi, Sydney Coalfield. 20–35 cm above Lloyd Cove Seam, Morien Group (upper Westphalian D).
2. 984GF-267 (9 slides) Point Aconi, Sydney Coalfield, Point Aconi Seam, Morien Group (lower Cantabrian).
3. 983GF-257 (6 slides) Brogan's Pit West, near Point Aconi, Sydney Coalfield . 1·5–2·0 m above an unnamed seam, which occurs *c.* 8 m above the Lloyd Cove Seam, Morien Group (upper Westphalian D).

N. scheuchzeri Hoffmann
1. 980GF-588 (12 slides) Brogan's Pit, near Point Aconi, Sydney Coalfield. 10–20 cm above an unnamed seam, which occurs *c.* 8 m above the Lloyd Cove Seam, Morien Group (upper Westphalian D).
2. 985GF-245 (14 slides) Point Aconi, Sydney Coalfield. Point Aconi Seam, Morien Group (lower Cantabrian).

SAARLAND COALFIELD
N. ovata Hoffmann var. *simonii* (Bertrand)
1. C/4146 (1 slide) Friedrichsthal Colliery, Friedrichsthal, Saarland. Kallenberg Seam, Luisenthal Formation (lower Westphalian D).
2. C/5037 (1 slide) Göttelborn Colliery, near Friedrichsthal, Saarland. Elizabeth Seam, Heiligenwald Formation (middle Westphalian D).
3. C/4894 (3 slides) Same locality and horizon.
4. C/5224 (4 slides) Reden-Flamm Colliery, near Friedrichsthal, Saarland. Grubenwald Seam, Heiligenwald Formation (lower Westphalian D).
5. C/5215 (3 slides) Same locality and horizon.
6. C/3638 (4 slides) Itzenplitz Colliery, near Friedrichsthal, Saarland. Kallenberg Seam, Luisenthal Formation (lower Westphalian D).

N. ovata Hoffmann var. *sarana* (Bertrand)
1. C/5 (9 slides) Kohlwald Colliery, near Neunkirchen, Saarland. Huyssen Seam, Heiligenwald Formation (upper Westphalian D).

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